A REVISION OF FAMILY PLEUSTIDAE (AMPHIPODA: GAMMARIDEA) PART I. SYSTEMATICS AND BIOGEOGRAPHY OF COMPONENT SUBFAMILIES

E. L. Bousfield[1] and E. A. Hendrycks[2]

ABSTRACT

The amphipod family Pleustidae is revised on the basis of extensive material obtained from the North American Pacific coastal marine region and from other sources, and of the pertinent world-wide literature. The world fauna now totals 145 species and subspecies in 38 genera and 12 subfamilies of which 43 species, 18 genera, and all 12 subfamilies are new . The family Pleustidae is redefined on the basis of taxonomic characters both newly recognized and previously utilized, and the subfamily components are diagnosed.

The previous heterogeneous assemblage of genera and species is herewith grouped in subfamilies that are both internally consistent, and externally interrelated. The new subfamilies are: Atylopsinae (TYPE species - *Atylopsis emarginatus* Stebbing, 1888); Austropleustinae (TYPE species - *Austropleustes cuspi-datus* K. H. Barnard, 1931); Stenopleustinae (TYPE species - *Stenopleustes malmgreni* Boeck 1871); Mesopleustinae (TYPE species - *Mesopleustes abyssorum* Stebbing, 1888); Pleustoidinae (TYPE species - *Pleustoides carinatus* Gurjanova, 1972); Eosymtinae (TYPE species - *Eosymtes minutus*, new genus, new species); Pleusymtinae (TYPE species - *Pleusymtes glaber* Boeck, 1871); Dactylopleustinae (TYPE species - *Dactylopleustes echinoicus* Tzvetkova, 1975); Pleustinae (TYPE species - *Pleustes tuberculatus* Bate, 1858); Pleusirinae (TYPE species *Pleusirus secorrus* J. L. Barnard, 1969); Neopleustinae TYPE species - *Neopleustes pulcheuus* Kroyer, 1842); and Parapleustinae (TYPE species - *Parapleustes gracilis* Buchholz, 1874).

Principal taxonomic characters utilized in diagnosing subfamilies are described and figured. Phyletic ordering of character states was determined mainly by comparison with those of presumed ancestral "outgroup" members of superfamily Eusuoidea, and by accepted precedent within the literature. The phyletic relationships of the subfamilies were analyzed on both phenetic and cladistic bases. The two results were somewhat similar over all but, in detail, the cladistic groupings appeared to be more natural and more consistent with corresponding biogeographic characteristics. Full descriptions of component genera and species and details of their distributional ecology, are being published in a series of monographic papers elsewhere (proposed for subsequent issues of this journal).*

Morphological and biogeographical analyses of the world-wide fauna revealed two major groups within the Pleustidae: (1) an older, more primitive, and deeper water Mesozoic fauna that is now relict in Indo-Pacific and southern oceans with an outlier in the North Atlantic, and (2) a younger, more advanced, and more eulittoral fauna that is richly diverse in the Holarctic and is centred in the cold-temperate North Pacific marine region. Indirect evidence suggests an early Mesozoic origin and evolution of family Pleustidae, and a post-Tethyan evolution and dispersal of the more advanced subfamilies within the holarctic region. A few members of both primitive and advanced groups have also penetrated the deep sea.

INTRODUCTION

The gammaridean amphipod family Pleustidae was proposed by T. R. R. Stebbing (1906) to encompass several genera that had previously been referred to the family Paramphithoidae. The new family included about 22 species, in the genera *Pleustes* Bate, 1858; *Parapleustes* Buchholz, 1874; *Stenopleustes* Sars, 1895; *Mesopleustes* Stebbing, 1899; *Sympleustes* Stebbing, 1899; and *Neopleustes* Stebbing, 1906. As a result of revisionary work during the next 60-70 years (e.g. Gurjanova, 1951, 1972; Barnard & Given, 1960; Barnard, 1969a) the recognized world fauna has more than tripled, to about 71 species in 13 genera. The additions included *Austropleustes* K. H. Barnard, 1931; *Parepimeriella* Schellenberg, 1931; *Pleusymtes* J. L. Barnard, 1969a; *Pleusirus*, J. L. Barnard, 1969b; *Pleustoides*, Gurjanova, 1972; *Pleustomesus* Gurjanova, 1972; and *Pleustostenus* Gurjanova, 1972. From then until the commencement of this study in 1984, about a dozen new species and the genera *Dactylopleustes* Karaman & Barnard, 1979 and T*epidopleustes* Karaman & Barnard, 1979, have been added, for a combined total of about 82 species in 15 genera.

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*Units include: Part II, Subfamilies Pleustinae, Dactylopleustinae and Pleusirinae; Part III, Subfamilies Atylopsinae, Austropleustinae and Stenopleustinae; PartIV, Subfamilies Mesopleustinae, Pleustoidinae, Eosymtinae and Pleusymtinae; and Part V. Subfamilies Neopleustinae and Parapleustinae.

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1 **Royal British Columbia Museum, Victoria, B. C. Canada V8V 1X4**
2 **Canadian Museum of Nature, Ottawa, Ontario, Canada K1P 6P4**

Thus, until very recently, the family Pleustidae was viewed as a relatively small to medium-sized group of benthic detritivores and micro-predators, occurring mainly in arctic and cold-temperate seas of the northern hemisphere (see Bousfield 1982a). The group is characterized by a generally dorsally toothed or carinated, deep-plated body morphology, and mouthparts and gnathopods trending to specialization for carnivory and raptorial feeding behaviour. The Pleustidae was positioned initially as the most primitive member of superfamily Leucothoidea by Bousfield (1979, 1982a, 1983). However, in several important respects the component members of family Pleustidae, especially the more primitive types, retain some characters that are little modified beyond those of families of the Eusiroidea; that superfamily is possibly ancestral to the Pleustidae and the other leucothoidean families.

Examples of plesiomorphic character states, common to some members of eusiroidean families and the Pleustidae are: rostrate heads, homopodous peraeopods, slender and subequal gnathopods, and lanceolate rami of the uropods. These character mixes also contributed to earlier difficulties in placing some genera (e.g. *Harpinioides, Atylopsis, Parepimeriella* and *Pleustoides)* within the proper family and superfamily (e.g., in Barnard, 1969a; Barnard & Karaman, 1991).

Since 1955, collecting expeditions of the National Museum of Natural Sciences (e.g.Bousfield, 1958, 1963, 1968, Bousfield & McAllister, 1963; Bousfield & Jarrett, 1981) have resulted in a wealth of new pleustid material from the Pacific coast of Canada and adjacent regions. This material has since been studied in detail by the present authors. It yielded 54 species in 25 genera of which 41 species and 15 genera are new.

In order to classify (in natural and manageable fashion) these new and previous world-wide taxa, now consisting of about 145 species and subspecies in 38 genera, the present authors have followed the model of Barnard and Drummond (1978). Their single-volume treatment of a large, mainly new fauna of phoxocephalid amphipods from south-eastern Australia necessitated the formal subdivision of family Phoxocephalidae into several subfamily units. These have since been expanded and modified to accommodate the world-wide fauna.

The present monographic treatment of family Pleustidae will appear in a five-part series. This paper (Part I) redefines the family Pleustidae, diagnoses the subfamilies, analyses their taxonomic and biogeographic relationships, and reconstructs probable evolutionary pathways to account for their present diversity and distribution. Diagnoses of generic and species components, and distributional-ecological data. for the individual subfamilies are presented elsewhere (Bousfield and Hendrycks, in prep., parts II, III, IV, and V).

ACKNOWLEDGEMENTS

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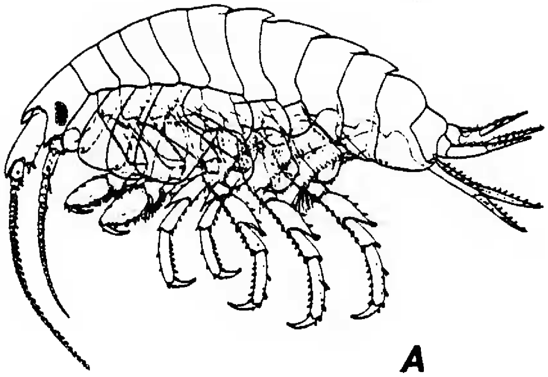
LEGEND FOR FIGURES (The following attributes to unpublished work are employed:

* Bousfield & Hendrycks, Part II, in prep.
! Bousfield & Hendrycks, Part III, in prep.
# Bousfield & Hendrycks, Part IV, in prep.
+ Bousfield & Hendrycks, Part V, in prep.

Fig. 1. Subfamilies of Pleustidae: Representative Species (SEE PAGE 19 - OPPOSITE)

A, B: PLEUSYMTINAE (New genus, new species, #; *Pleusymtes,* new species, !)
C : ATYLOPSINAE (*Atylopsis procerus*) (after Andres, 1986)
D : PLEUSIRINAE (*Pleusirus secorrus*) (after *)
E, F: PLEUSTINAE (*Pleustes,* new species *; new genus, new species *)
G : PARAPLEUSTINAE (New genus, new species +)
H : EOSYMTINAE (*Eosymtes,* new species#)



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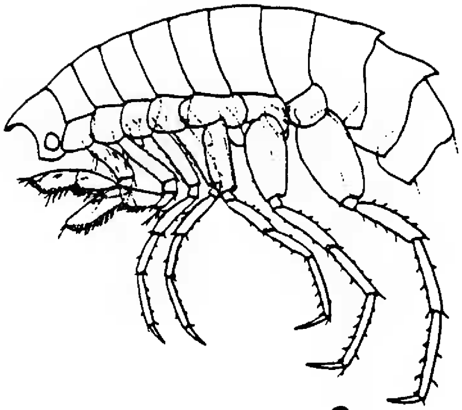

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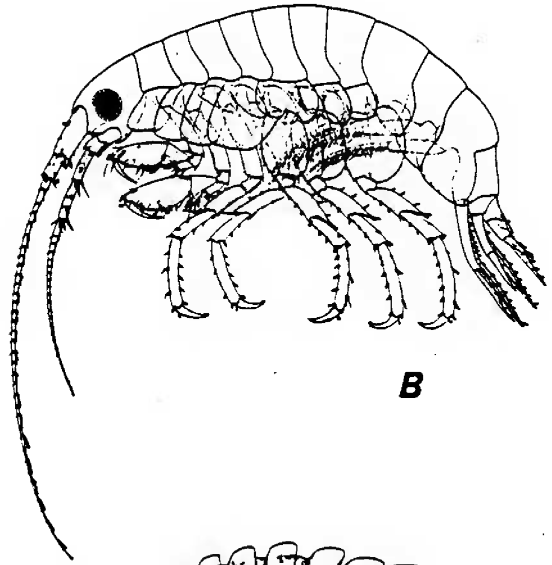

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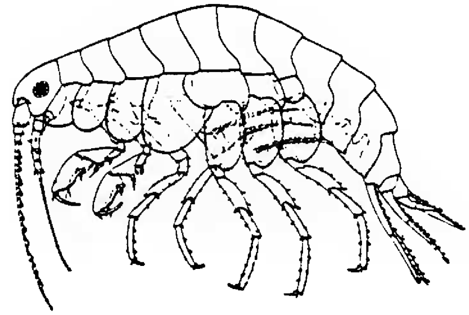

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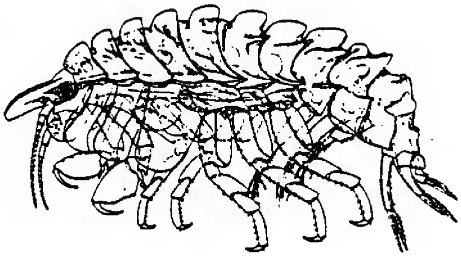

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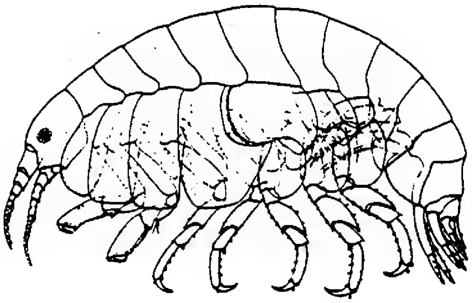

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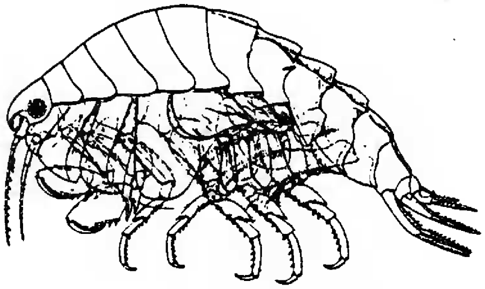

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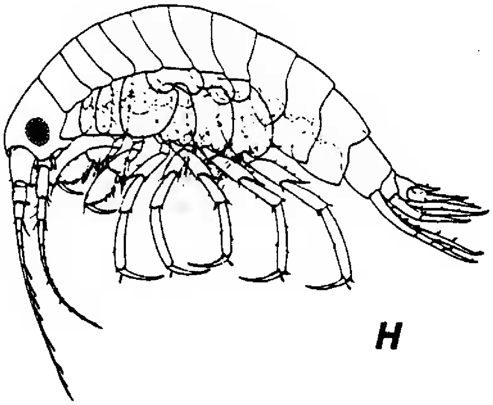

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SYSTEMATICS

TAXONOMIC CHARACTERS AND CHARACTER STATES OF THE PLEUSTIDAE

The amphipod family Pleustidae has been viewed previously as a relatively small to medium-sized group of species. Taxonomically usable or diagnostic characters were relatively few, and character states of the general body, appendages, and mouthparts varied little (e.g. Barnard, 1969a, andp. 20 below). The present study reveals, however, that the family is one of the larger sub-units of suborder Gammaridea (145 species and subspecies) with such rich diversity of taxonomic characters, and breadth of pertinent character states, that 38 genera and 12 subfamilies are required to encompass them. This diversity compares favourably with that found by Barnard and Drummond (1978) in their comprehensive taxonomic analysis of the Phoxocephalidae, a primitive fossorial family of comparable size. In particular, the mouthpart morphology of these two groups of detritivores and micro-carnivores varies in remarkably similar ways (form of the mandibular molar, lower lip, maxillipedal palp) even though they occupy essentially different habitats. Granted, part of this diversity is attributable to the expanded definition of Pleustidae (herein). This definition encompasses genera and higher units that are either aberrant and/or new (e.g. within Eosymtinae) or had previously been included in other superfamilies (e.g.*Atylopsis* within Eusiroidea). Also, some were not clearly allocated at family or superfamily level (within *Incertae Sedis).* However, the main factors accounting for this diversity are: (1) the incorporation of many new pleustid genera and species from the North Pacific region, and (2) the more comprehensive description and analysis of all body parts as detailed below and in subsidiary publications (Bousfield & Hendrycks, in prep., Parts II-V). The diversity of some of the principal taxonomic characters is indicated in figures 1-7.

The use of taxonomic characters in diagnosing and phyletically relating subgroups within Pleustidae is complicated by the phenomenon of morphological convergence. As Barnard and Drummond (1978) discovered, this factor more than any other had led to the previous unsatisfactory state of classification within the northern phoxocephalids. This was rectified by full analysis of the more primitive groups of the southern hemisphere, especially of the Australian region. Although the phoxocephalids and pleustids appear to be of comparable diversity and antiquity, the modern pleustid groups of the northern hemisphere have revealed the extent of morphological convergence, and led to the development of a more realistic natural classification of the world fauna of Pleustidae. However, these general conclusions may require modification as new information comes to hand. Further study of the aberrant and primitive pleustids of Indo-Pacific marine regions, and of northern pleustids with specialized habitats and life styles, are much needed in this regard.

Sexual Differentiation

Within the Phoxocephalidae, the sexes are strongly dimorphic; they swarm and mate synchronously in the water column (Bousfield, 1979, 1982a). Within the Pleustidae, however, sexual dimorphism is little evident. There is apparently no reproductive swarming phase, and mating within most subfamilies takes place probably on or near the bottom. Pre-amplexus *(sensu* Borowsky, 1984), possibly of short duration, may take place in some pleustid taxa in which the gnathopods are conspicuously sexually dimorphic (as in some Parapleustinae). Such inference, however, requires confirmation from actual behavioural studies.

Males tend to differ only slightly from females in superficial characters such as body size, head structures, gnathopods, and other appendages. Thus, in males, the body is generally smaller and more slender, but the eyes are usually larger, the rostrum stronger, antenna 1 has more sensory aesthetascs, antenna 2 is often more setose, and the gnathopods are relatively larger and more powerful. In addition, the peraeopods (segments, especially dactyls) are more slender, pleopods 2 and 3 are occasionally modified, the uropod rami are more slender, and the telson is often longer and more slender than in corresponding females. Since these differences are relatively slight, and because the female is usually larger, and more frequently encountered in

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Fig. 2. Subfamilies of Pleustidae: Representative Species. (SEE PAGE 21 - OPPOSITE)

I, J: STENOPLEUSTINAE *(Sympleustes latipes* - after Lincoln, 1979; Sars, 1895; S. *malmgreni* - after Barnard, 1969a; Sars, 1895).

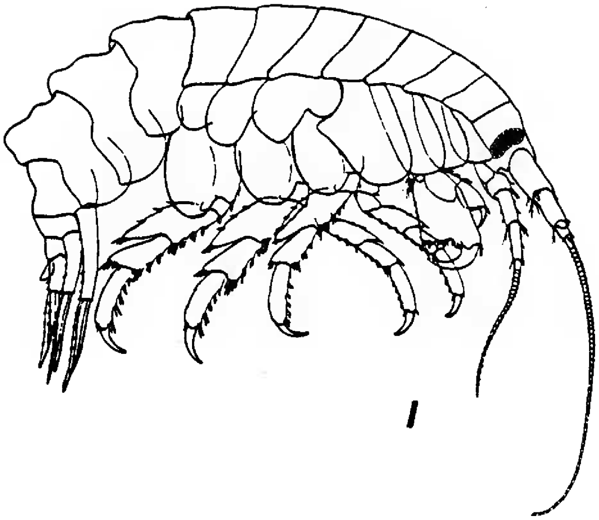
K, L: PARAPLEUSTINAE *(Parapleustes,* new species +; New Genus, new species, +)

M: AUSTROPLEUSTINAE *(Tepidopleustes honomu* - after Barnard, 1971)

N: DACTYLOPLEUSTINAE *(Dactylopleustes,* new species*)

O: PLEUSTOIDINAE *(Pleustoides carinatus* - after Gurjanova, 1972)

P: MESOPLEUSTINAE *(Mesopleustes,* new species, #)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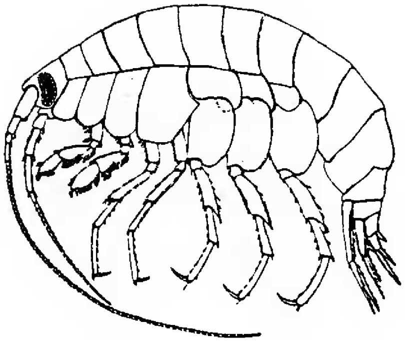
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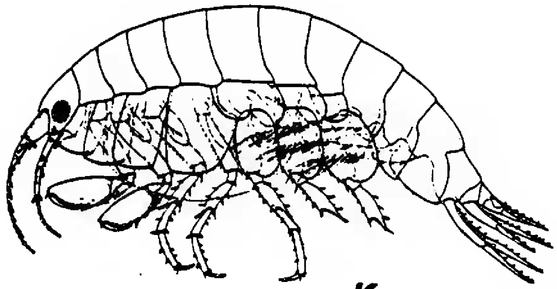
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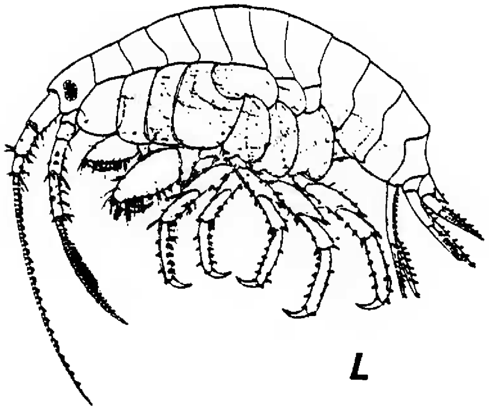
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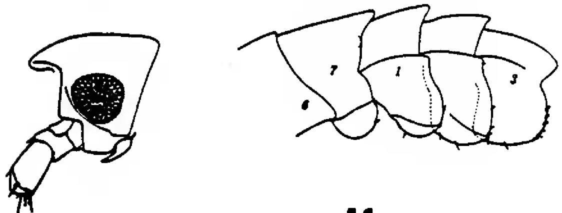

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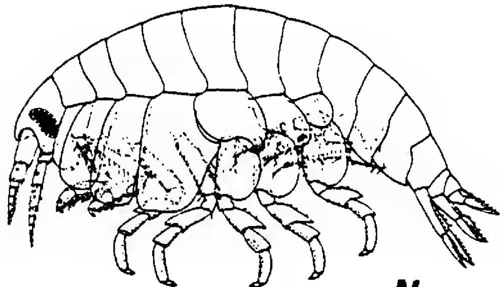
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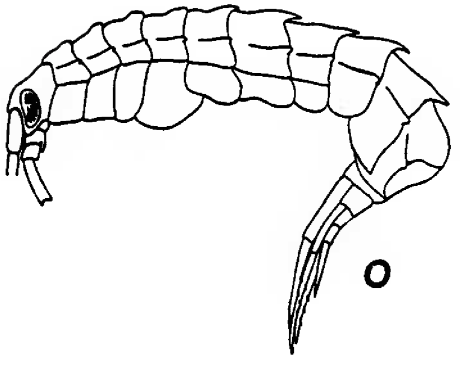
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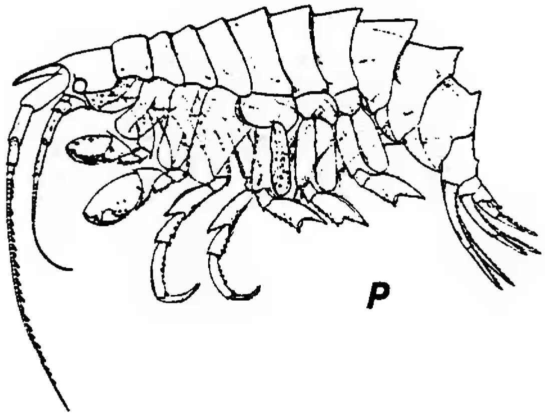
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field samples, the following diagnoses (and more detailed descriptions elsewhere) are based on the female sex, unless otherwise designated.

Body Form

Pleustids are small to medium-sized (2.0 - 30.0 mm) amphipods in which the dorsal and/or lateral surfaces of the peraeon and pleon are often variously carinated, toothed, or mucronate (Figs. I A,C,E,F; Figs. 2I,M,O,P). Only in Eosymtinae, Pleusirinae, and most Parapleustinae and Pleusymtinae are surface processes lacking. In pleustids, the dorsal margin of urosome 2 is narrow, and often totally occluded by segments 1 and 3, especially in more advanced subfamilies (Figs. I A,B,D,G; Figs. 2K,L). This feature, like the median posterior cusps on coxae 2-4 of some Pleustinae, and the plumose inner marginal seta(e) of maxilla 2, are reminiscent of many Talitroidea.

Body Colour

Pleustids are among the most beautiful and strikingly pigmented amphipods (Bousfield, 1985). At least two species in two different subfamilies bear the appellation ' "pulchellus". Subcutaneous pigmentation provides ground colouration that may range from almost black to pure white; on such background may be superimposed the changeable colour and size of epicuticular chromatophores that contribute to the mottled and speckled appearance of certain sand and gravel-dwelling species within the Pleusymtinae and Parapleustinae. The striking body colouration of members of Pleustinae and Parapleustinae that occupy bottom sites open to easy fish predation, may function in warning potential predators of distasteful or poisonous body compounds.(e.g. terpenes) of types recently investigated in eastern Pacific invertebrate animals by Andersen (1988). Pleustids members of the amphipod community are not heavily preyed upon (Nagata, 1966). Other types of body colouration (banding) combined with specialized body form and posture (e.g. in Pleustinae), enable the amphipods to imitate mitrellid snails in classical Batesian mimicry (Crane, 1969; Field, 1974).

Rostrum

The rostrum is generally medium, down-curved distally, but does exceed the antero-lateral head lobe (Figs. 1A,C,D,F,H; 2I,J,M,N; 3E). In some of these (e.g. in Neopleustinae), the rostrum appears as a short extension of the mid-dorsal head crest.

In a few, mainly advanced groups, the rostrum is shorter than the lateral head lobe (e.g. Figs. I B,G; 2K,L,O; 3D). However, in Mesopleustinae, Pleustinae, and some Pleusymtinae *(Pleustomesus)* the rostrum is strongly developed, its length more than half that of the dorsal margin of the head itself (Figs. IE, F; 2P; 3A-C). In Pleustinae, the rostrum is typically sexually dimorphic, and is longer and more slender in the male than in the corresponding female.

Lateral Head Lobe

Usually acute (Fig. IA,G; 2K,O,P) but may be sub-acute or rounded (Figs. ID,H; 2L,N). Its anterior margin is usually smooth and even, but may be weakly incised, with even a faint trace of the "pontogeneiid" cleft (Fig. 2I - some Stenopleustinae). The inferior antennal sinus is often long and shallow (Figs. 1 H; 20,P), but may be deep and the lower cusp acute (Figs. 1 A, 1 B, 2L - in Pleusymtinae, Parapleustinae).

Eyes

The paired lateral eyes are typically large, ommatidial, and pigmented. They may be sub-rectangular or sub-rhomboidal in outline (Fig. 1B,H,2M), reniform (Figs. 21,J,N,O), oval or roundish (Figs ID,G), or unpigmented (Fig.2P).

Fig. 3. Subfamilies of Pleustidae: Heads (A-E); Coxal Plates, (F-M); Accessory flagellum (N,O); Telson (dorsal and lateral aspects: P-X) (SEE PAGE 23 - OPPOSITE)

Heads (lateral view)

A,B : PLEUSTINAE *(Pleustes,* new species *; *Pleustes,* new species *)
C : PLEUSTINAE (New genus, new species *)
D : PARAPLEUSTINAE (New genus, new species +)
E : PLEUSYMTINAE (New genus, new species *)

Coxal Plates

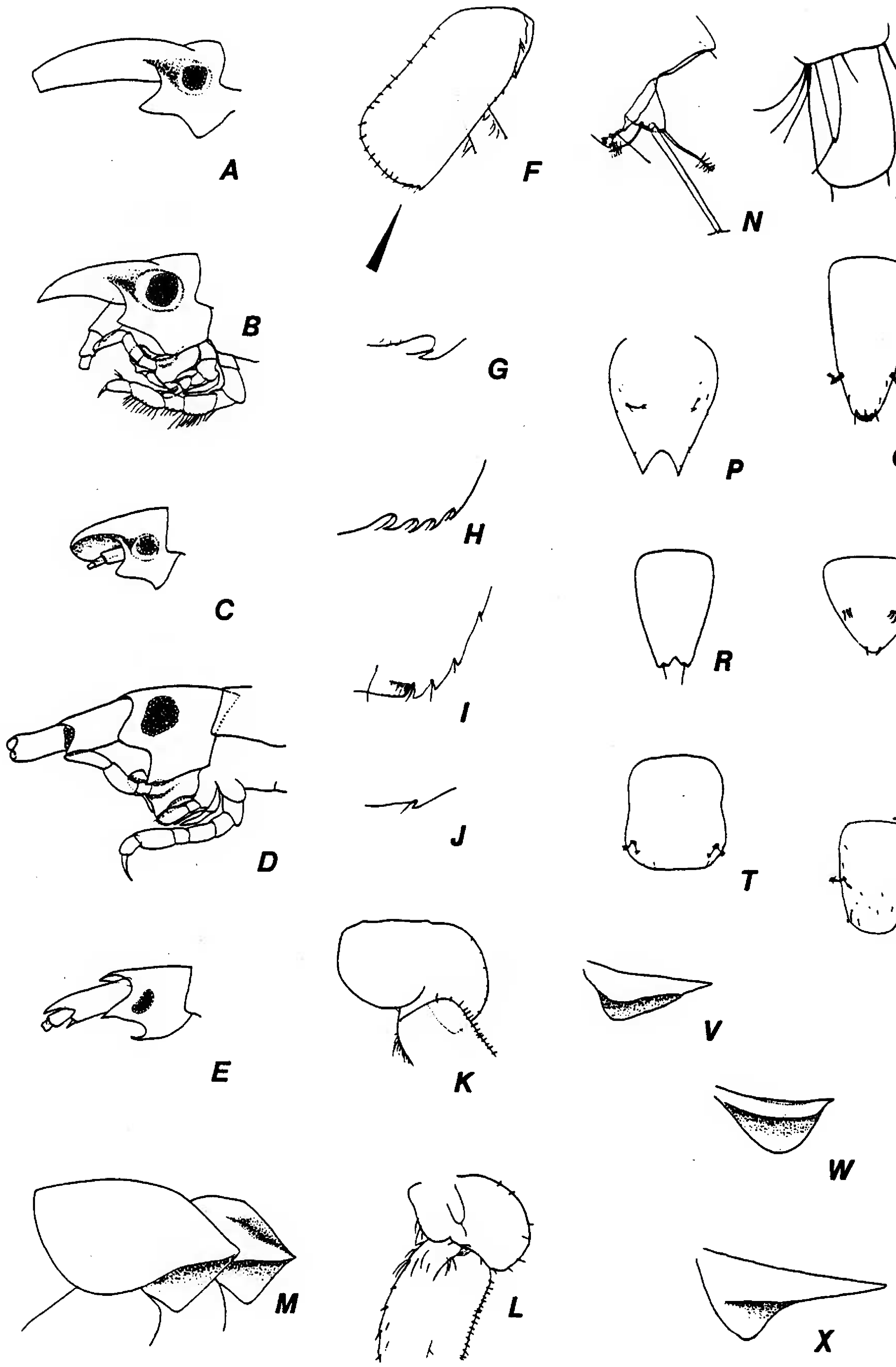
(Coxae 1-3: F-J; coxa 5: K; coxa 6: L; coxae 6-7: M)
F : PLEUSYMTINAE *(Pleusymtes coquillus* - after Barnard, 1971)
G : PLEUSYMTINAE (New genus, new species #)
H : EOSYMTINAE *(Eosymtes,* new species #)
I, J: PARAPLEUSTINAE (New genus, new species +; *"Parapleustes" oculatus* Holmes, 1908 +)
K, L: PLEUSYMTINAE *(Pleusymtes coquillus* - after Barnard, 1971)
M : PLEUSTINAE *(Pleustes* sp. *)

Accessory Flagellum

N : PARAPLEUSTINAE (New genus, new species +)
O : INCERTAE SEDIS (*Harpinioides drepanocheir*- after Stebbing, 1888)

Telson

P : ATYLOPSINAE (*Atylopsis procerus* - after Andres, 1986)
Q : PARAPLEUSTINAE (New genus, new species +)
R : INCERTAE SEDIS (*Harpinioides drepanocheir* - after Stebbing, 1888)
S : AUSTROPLEUSTINAE (*Tepidopleustes honomu* - after Barnard, 1970)
T : PLEUSTINAE (*Pleustes* sp. *)
U : PLEUSYMTINAE (New genus, new species #)
V : PARAPLEUSTINAE (*"Parapleustes" oculatus* Holmes, 1908 +)
W : STENOPLEUSTINAE (*Stenopleustes pulchellus* Sars, 1895 !)
X : PLEUSTINAE (*Pleustes* sp. *)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Antenna 1

Usually elongate and longer than antenna 2, with slender flagellum, the segments of which bear short, slender aesthetascs, more richly so in the male (Figs. 1 A,B; 21,J,L,P). Very rarely (in some Atylopsinae, Stenopleustinae) the basal flagellar segments are conjoint and may bear a few short transverse rows of aethetascs, forming what may be a vestigial callynophore (Lowry, 1986). Peduncular segment 1 is normally elongate, often with antero-distal or postero-distal processes (Figs. 40, P). Peduncular segments 2 and 3 are long, plesiomorphically (Figs. 21,J,L,P) but become variously shortened apomorphically (Figs. lD, F,G). The accessory flagellum is typically minute (Fig. 3N), vestigial, or totally lacking, rarely l-segmented and distinct (Fig. 3).

Antenna 2

Usually slender, and shorter than antenna 1, with slender, weakly spinose (rarely setose) peduncle and flagellum. The basal segment is large, rounded anteriorly, and the gland cone of segment 2 is usually large, distinct, and subparallel to the posterior margin of segment 3. In a few instances (Figs. lE, F. G; 2N) the antennae are short, few-segmented, and subequal.

Buccal Complex

The buccal mass of most pleustids is retrogressed somewhat posteriorly beneath the head (Figs. 3B,D; Fig. 7). The buccal complex is shallow in most primitive subfamilies (Fig 7) but medium-deep in higher subfamilies (Figs. 3B,D).

Upper Lip

In higher subfamilies, the upper lip is variously deeply cleft, with sloping sides; the lobes are distinctly asymmetrical (Figs. 4E-G). In primitive subfamilies, the distal margin is shallowly notched (depth less than width), nearly smooth, and the lobes are subequal (Figs. 4A-D). The epistome is usually ridged medially, but it is rounded in front, not acutely produced (Fig. 4C).

Lower Lip

In higher subfamilies the inner lobes are flat and shallow; the outer lobes are small, rounded, oblique. and widely separated (Figs. 4M, N). In lower subfamilies, the inner lobes are indistinct or small and narrow, and the outer lobes are large and closely approximated (Figs. 4H,I). In all instances, the mandibular lobes are relatively short and the wings rounded. Intermediate conditions occur in the intermediate families (Figs. 4J-L).

Mandible

The pleustid mandible exhibits a variety of biting and grinding surfaces, indicating a corresponding diversity of feeding types. The mandibular body is of medium size, slender, and generally tapers distally to the multi-cuspate cutting incisors. The bite is guided by the lacinia mobilis, the right incisor fitting and locking between the left incisor and left lacinia mobilis, in the manner indicated by Dahl and Hessler (1981).

Lacinia Mobilis

The left lacinia is multi-dentate; the usual number of teeth ranging from 6-12 (Figs. SA,F,H), rarely as few as 5 (some Atylopsinae), but may be more than 20 (in some Parapleustinae). The teeth may be regular (Figs. SA,H) or uneven (Fig. SF). The right lacinia is present only in the in the primitive subfamilies. It may be tricuspate (Atylopsinae), blade-like, or bicuspate (Fig. SD inset), spike-like, or otherwise reduced (Stenopleustinae).

Spine-Row

The blades of the spine-row serve primarily to push food particles toward the grinding molar, and/or mouth opening K: (Dahl and Hessler, 1981). In many pleustids, the blades are numerous (6-15), slender, distally simple or weakly pectinate (Figs. SA,B,E). The distal blades of the spine-row are usually largest and most strongly modified. In some groups, especially those in which a true right lacinia is lacking (e.g. Pleusymtinae) the distal-most blade(s) may be broad and chisel-shaped, and serve as a false lacinia. In some groups (Figs. 5B,H), the supernumerary slender setae (between the blades) may form small clusters next to the left lacinia. In other groups, particularly those with modified or non-triturating molar surfaces, the blades are fewer and often thickened, stiffened, and heavily pectinate distally (Figs. 5B,C,D,H). In the most specialized feeding types (within

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Fig. 4. Subfamilies of Pleustidae. Mouthparts: Upper Lip (A-G); Lower Lip (H-N); Antenna 1, peduncle 1 (O-P). (SEE PAGE 25 - OPPOSITE).

Upper Lip

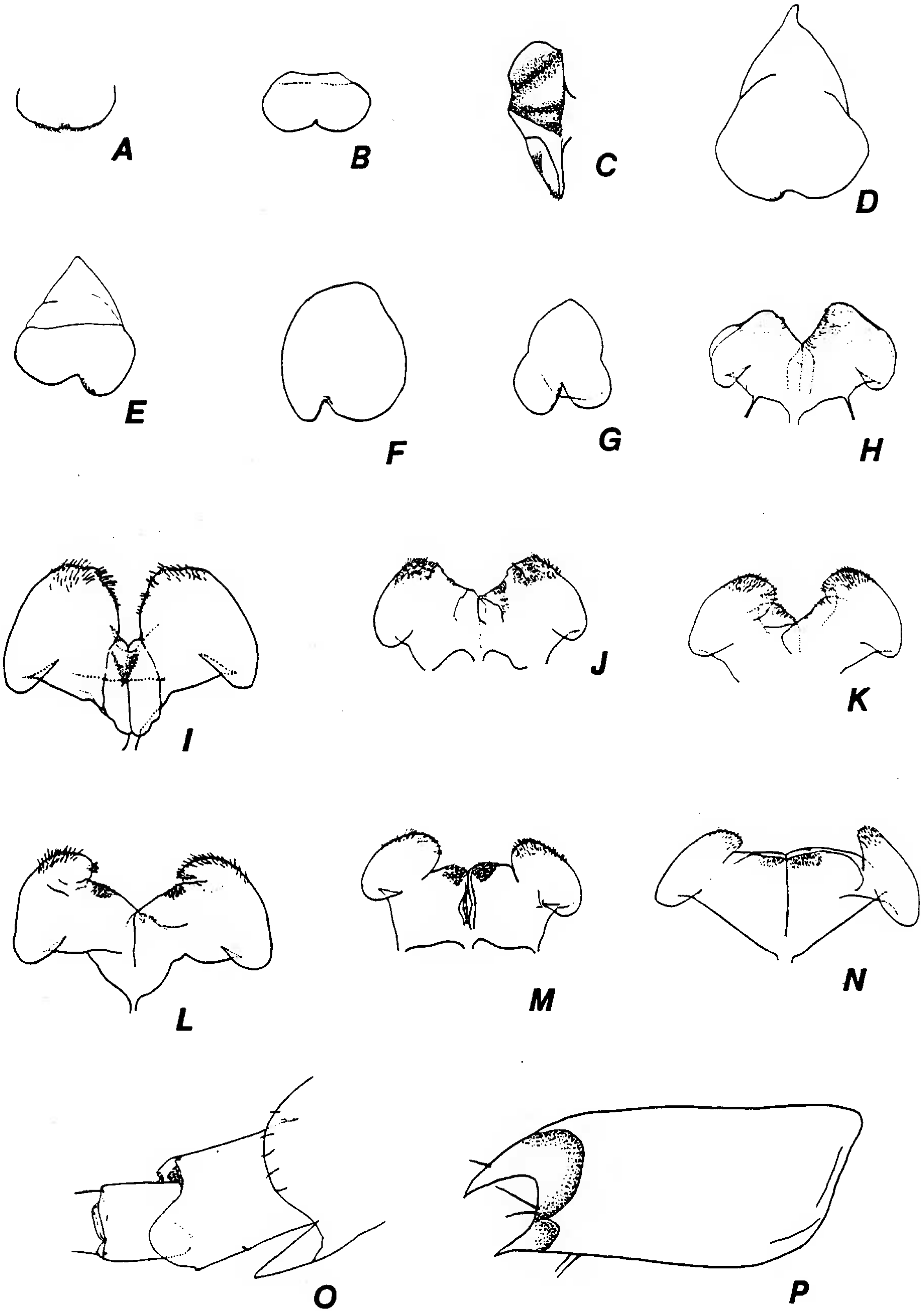
A : ATYLOPSINAE (*Atylopsis procerus* - after Andres, 1986)
B : DACTYLOPLEUSTINAE (*Dactylopleustes*, new species *)
C : PLEUSTINAE (*Pleustes* sp. *)
D : EOSYMTINAE (*Eosymtes*, new species #)
E : PLEUSYMTINAE (New genus, new species #)
F : STENOPLEUSTINAE (*Stenopleustes monocuspis* Barnard and Given 1960 !)
G : PARAPLEUSTINAE (*"Parapleustes" oculatus* Holmes,1908 +; new genus new species +)

Lower Lip

H : MESOPLEUSTINAE (*Mesopleustes* sp. #)
I : EOSYMTINAE (*Eosymtes*, new species #)
J : PLEUSTINAE (*Pleustes* sp. *)
K, L : PLEUSYMTINAE (New genus, new species #)
M, N: PARAPLEUSTINAE (*"Parapleustes" oculatus* Holmes,1908 +)

Antenna 1, peduncle 1

O : PLEUSYMTINAE (New genus, new species #)
P : EOSYMTINAE (*Eosymtes*, new species #)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Parapleustinae) the blades may be very short, stout and heavily chitinized or mineralized, with a flattened apex forming an effective "molarized" grinding surface (Fig 5F). Intermediate forms of this type occur within the Parapleustinae.

Molar

The mandibular molar provides one of the principal bases for differentiation of pleustid subfamilies. Six principal types are recognized: (1) large, columnar; triturating (grinding) surface fully ridged (Fig. 5A); (2) large, columnar. triturating surface with smooth (unridged) central core, and ridged or spinose periphery (Figs. 5C,D); (3) compressed or narrowing distally; grinding surface "cobbled", or granular, with or without marginal spines (Figs. 5G,H); (4) columnar, with smooth or pavement-like grinding surface, and uniformly sharp edges (Fig. 5B); (5) non-triturative; apex inflated, margin rounded, smooth, with no trace of ridges or teeth (Fig. 5E); (6) non-triturative; apex small, conconical, stub-like, setulose (Fig. 5F). In plesiomorphic variants of (6) (e.g. some Neopleustinae), the molar body is less reduced, and the apex may retain minute spines and non-functional ridges. In variants of (1) and (2) above, the molar bears a chitinized distal molar hump (or knob), and antero-medially a plumose flagellum, both typical of eusiroidean and talitroidean molars, but lacking in most leucothoidean molars. A distal molar setal tuft (primordial molar flake of Conlan, 1983; Lincoln & Lowry, 1984) is variously present in the primitive subfamilies (above), and in the Stenopleustinae (Figs. 5A,D).

Palp

The mandibular palp is 3-segmented, the segments typically slender and elongate (Fig. 7 - Eosymtinae). In some groups (Neopleustinae, Pleusirinae, some Parapleustinae) the palp is elongate, more than double the length of the mandibular body, but it is of normal size (to 1.5 times MD body) in most subfamilies. Segment 3 is usually as long as, or longer than, segment 2, slightly curved, with blunt apex bearing 4-5 long setae, and the posterior margin lined with a variable number of short to medium, pectinate setae and/or occasionally longer simple setae (Fig. 7). The "A" setae (Cole, 1980) are inserted very near the base of the segment and typically are restricted to a single seta (Fig. 7 - Eosymtinae). In the apomorphic condition, "A" setae are lacking entirely. In the plesiomorphic condition, two or more setae may occur in small basal clusters (e.g. in Atylopsinae, some Austropleustinae), or in clusters of up to 12 long setae (some Pleustinae). Segment 2 is slender, rarely broadened (as in eusiroideans) and the inner margin (especially distally) is armed with variable numbers of slender setae. Segment 1 is typically short, but occasionally elongate (as in Pleusirinae, some Neopleustinae).

Maxlla 1

The outer plate is medium short, not very broad, and typically bears 9 stout apical pectinate spines (Fig. 7 detail - Eosymtinae, most subfamilies). In the plesiomorphic condition, there are 11 spines (e.g. Atylopsinae, Mesopleustinae). In the apomorphic condition there are either few (6-7 in most Stenopleustinae) or many (15-20+ in some Dactylopleustinae and Parapleustinae); in the latter case the spine-teeth tend to be tall, simple, slender, and curved. The inner plate is small, ovate or triangular, and usually bears 1-2 (plesiomorphically 3-4, or apomorphically 0) apical setae. The palp is 2-segmented, typically slender, the apex exceeding the outer plate. The distal segment is armed apically with short stout spines and sub-apically with slender spines, and facially (often) with setules or pilosity. The proximal segment is short, but may have a disto-lateral wing-like expansion that may bear short setae (e.g. Pleustinae, some Stenothoinae, Neopleustinae).

Fig. 5. Mouthparts. Mandible (A-H); Maxilliped Palp (I-M); outer plate (N-O); Inner plate (P-R)

(SEE P. 27 - OPPOSITE)

Mandible

A : MESOPLEUSTINAE *(Mesopleustes,* new species #)
B : PLEUSYMTINAE (New genus, new species #)
C, D: EOSYMTINAE *(Eosymtes,* new species # showing left lacinia; New genus, new species # showing right lacinia)
E : DACTYLOPLEUSTINAE *(Dactylopleustes,* new species *)
F : PARAPLEUSTINAE (New genus, new species +)
G : STENOPLEUSTINAE *(Stenopleustes monocuspis* Barnard & Given, 1960); *Stenopleustes pulchellus* Sars, 1895 !)

Maxilliped palp

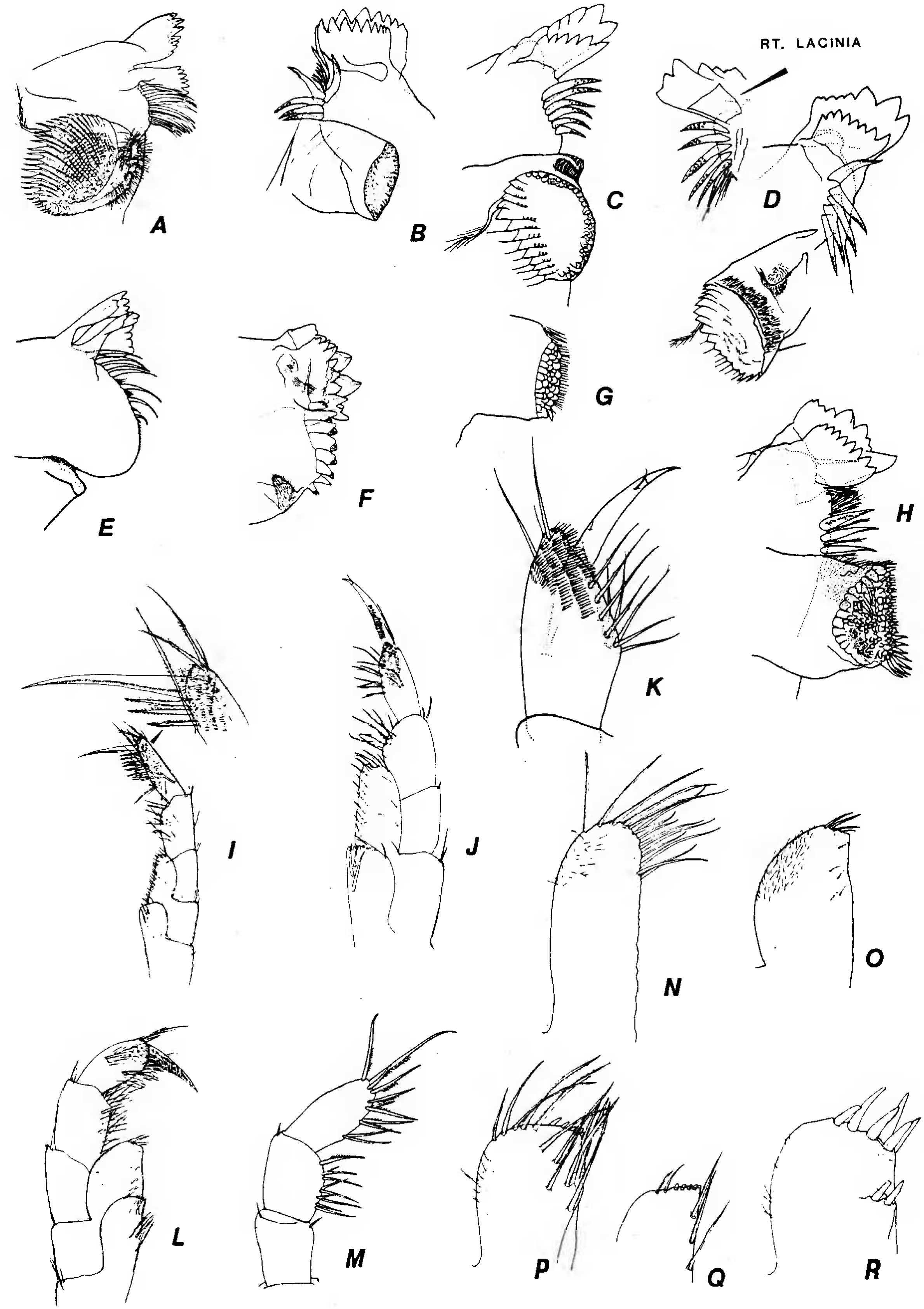
I : NEOPLEUSTINAE *(Neopleustes,* new species +)
J : PLEUSYMTINAE *(Pleusymtes coquillus,* - after Barnard, 1971)
K: STENOPLEUSTINAE *(Stenopleustes monocuspis,* Barnard & Given, 1960 !)
L : MESOPLEUSTINAE *(Mesopleustes,* new species #)
M : AUSTROPLEUSTINAE *(Tepidopleustes honomu* - after Barnard, 1970

Maxilliped outer plate

N : PARAPLEUSTINAE (New genus, new species +)
O : MESOPLEUSTINAE *(Mesopleustes,* new species #)

Maxilliped, inner plate

P, Q : PARAPLEUSTINAE (New genus, new species +; *"Parapleustes"oculatus* Holmes, 1908 +
R : PLEUSTINAE *(Pleustes sp: *)*


RT. LACINIA
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Maxilla 2

The plates are relatively small, the inner typically slightly shorter than the outer plate, and variously broadened medially (Fig. 7 detail - Eosymtinae). Both plates are apically armed with medium long stiff setae. The inner plate lacks the row of facial setae so conspicuous in eusiroidean family members; however, one or two large plumose inner marginal or submarginal setae occur in nearly all pleustid subfamilies. They are similar to those of talitroidean family members and may represent dislocated remnants of the presumed ancestral facial row.

Maxilliped

Characters of the maxilliped plates and palp are very important in pleustid classification. Three main types of outer plates are distinguished here: (1) broad, having the outer margin strongly arched and broadest medially (Fig. 5O); (2) narrow, columnar, having both inner and outer margins essentially straight and subparallel (Fig. 5N); and (3) intermediate, having the outer margin arched or curved distally but broadest basally (Figs. 5I,J). The inner margin is typically smooth and sharp and forms a cutting edge; although normally straight, it may be scalloped (some Stenopleustinae) or incised and bowed (as in Dactylopleustinae). It may be armed submarginally with few to many short setae (Figs. 5N,O).

The inner plate is typically shorter and broader than the outer, exceeding the base of the outer plate segment mainly in primitive subfamilies (Fig. 5L). The apex is typically subtruncate, and bears variable numbers of spines of two types: (1) heavy and stout (Fig. 5R); or (2) small, short, "button-like" (Figs. 5J,L,Q). Intermediate types also occur (Fig. 5P). The anterior face and inner margin bear few to several slender masticatory setae (Figs. 5J, L,P,Q) or 2-3 stiff, heavy, spines (Fig. 5R).

The palp is normally 4-segmented; segment 2 is normally longest. The dactyl is long, slender, and possesses micro-pectinate (Figs. 5J, L) but these are lacking in the austral group (Atylopsinae to Stenopleustinae) (Fig. 5K). The dactyl is occasionally small or lacking (Fig. 5M).

Segment 3 is of two main types: (1) apex oblique, extending distally beyond the base of the dactyl (Figs. 5K,1), or (2) apex truncate or gently rounded, not extending distinctly beyond the base of the dactyl (Figs. 5J,L). In several genera within Neopleustinae and Parapleustinae, the inner distal margin of segment 3 may be armed with stiff pectinate spines and short serrate teeth (Fig. 5(I) - detail). The distal medial surface usually bears numerous micro-pectinations arranged in short rows (Fig. 5 (I)).

Coxal Plates 1-4

The anterior coxal plates of pleustids are typically deeper than wide, and increase regularly in size posteriorly (Figs.1B,D,F; 2 I-L). Rarely are the plates small and shallow (Fig 1C). However, coxa 1 varies considerably in form. It may be markedly smaller than the others (Fig. 2N). The distal portion may be expanded broadly (Figs. 1E,F; 2L) or narrowing and bent forward (Figs. 2K,P). The lower margins of coxae 2-4 are often straight or nearly so (Figs. 1A,B,E-H; 2I, K,L,N) but may be rounded (Fig. 1D, 2J). In coxae with straight margins, the posterodistal corners of plates 1-3 bear one or more cusps or notches that are usually small (Fig. 3J), occasionally multiple (Figs. 3F,H,I), but may be conspicuous (Figs. 1A; 2K; 3G). Coxa 4 is normally strongly excavate posteriorly, shallowly (Figs. 1A,B,E; 2X, L,P) or occasionally deeply (Fig. 1G - some Parapleustinae), and may be produced as a distinct posterior process (Figs. 1 E,F; 2I,N).

Gnathopods 1 & 2

Typically they are strongly subchelate and subsimilar in form and size. Gnathopod 2 is usually slightly larger, the propod stronger, and the carpus shorter and deeper than in gnathopod 1 (Figs. 6G,H; J,K; Q,R). The basal segment of each gnathopod is relatively long and slender and protrudes below the coxal plates (Figs. 1 B,C; 2J). The posterior margin is nearly smooth, but the anterior margin is often heavily (Figs. 1E,F; 2J,N), setose distally or nearly bare (Figs. 1D,H; 2X,P). The ischium (segment 3) is always short, as in eusiroideans. The merus (segment 4) is also short; the postero-distal margin is usually rounded and setose (Figs. 6A,B; D,E; N; O,P) but may be produced in a sharp tooth or cusp (Figs. 6 G,H; J,K; L,M; Q,R).

Fig. 6. Subfamilies of Pleustidae: Representative types of gnathopods, and pleon plates 1-3. (SEE PAGE 29).

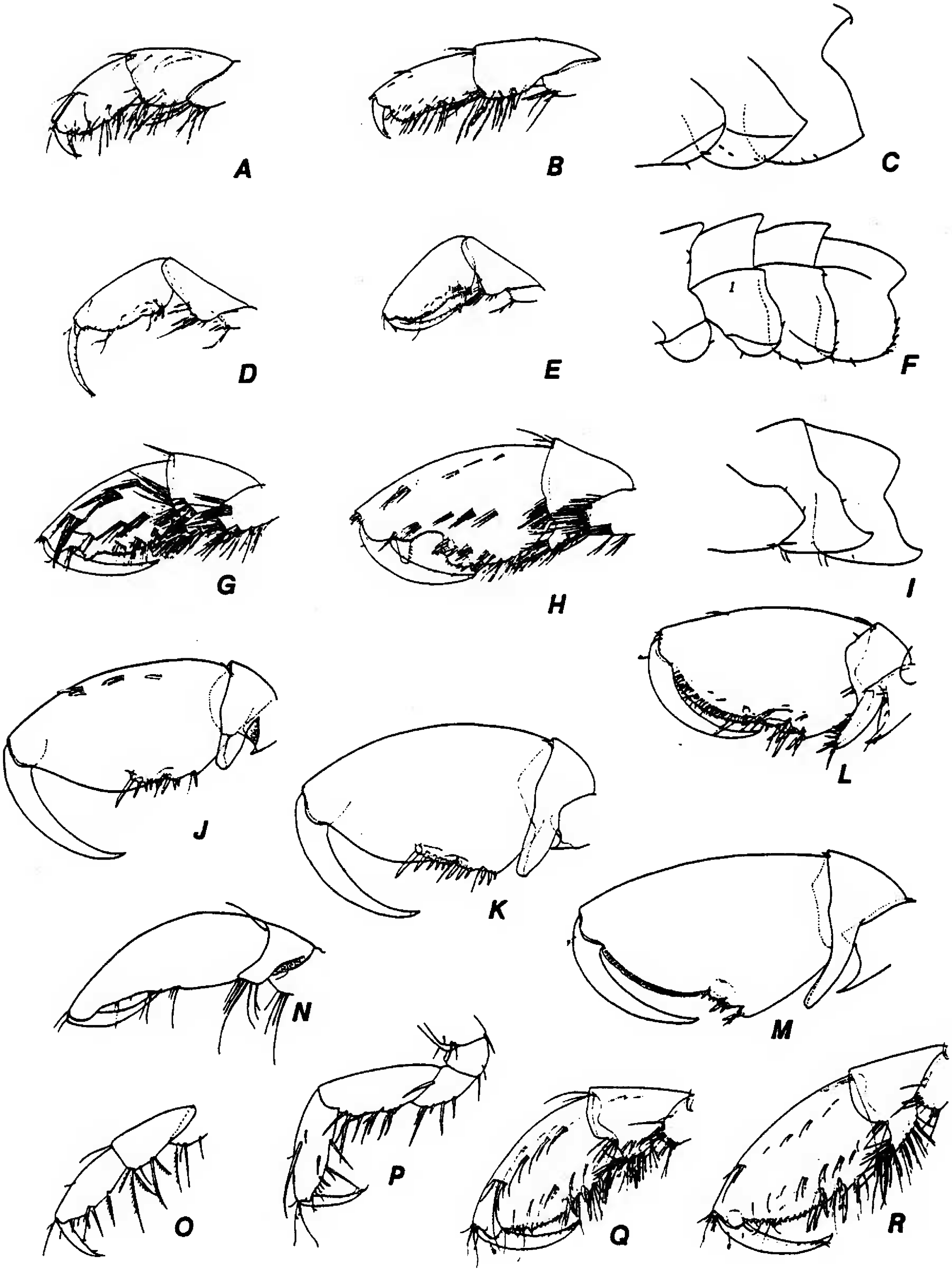
Gnathopods 1 & 2
A,B : DACTYLOPLEUSTINAE (*Dactylopleustes*, new species,)
D,E : PLEUSIRINAE (*Pleusirus secorrus*) (After *)
G,H : MESOPLEUSTINAE (*Mesopleustes*, new species #

J,K : PLEUSTINAE (*Pleustes* (new subgenus) sp.)

O,P : AUSTROPLEUSTINAE (*Tepidopleustes homonomu* - after Barnard, 1970)
Q,R : PLEUSYMTINAE (New genus, new species, !)

Gnathopod 1
N : *INCERTAE SEDIS*: (*Harpinioides drepanocheir* - after Stebbing, 1888)
Gnathopod 2
L,M : PLEUSTINAE (New genus, new species. *; *Pleustes*, new species *)

Pleon plates 1-3
C : PARAPLEUSTINAE (*"Parapleustes" derzhavini* - after Barnard, 1970)
F : AUSTROPLEUSTINAE (*Tepidopleustes honomu* - after Barnard, 1971)
F,I : PLEUSYMTINAE (*Pleusymtes coquillus* - after Barnard, 1971)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The plesiomorphic condition of the carpus is shallow and elongate, subequal to the propod, with long, shallow, setose or spinose posterior lobe (Figs. 6A,B; O,P). In the apomorphic condition, the carpus is short and deep, with a deep, narrow hind lobe that is often densely armed apically with rows of stiff setae and occasionally with pectinate spines (Figs. 6J,K; 3L,M). Intermediate stages are frequent (Figs. 1A,B; 2H; 6 Q,R - in many subfamilies). A second apomorphic condition is the "eusiroidean" form in which the carpus is long and very slender, with a small, shallow, weakly setose posterior lobe (Figs. 6D,E).

The plesiomorphic condition of the propod is also shallow and elongate, with a small, smooth, convex palm, and setose posterior margin (Figs. lC,G; 6A,B). This condition is conceivably secondarily derived or convergent in one genus of Parapleustinae (Fig. 6G). In the presumed plesiomorphic or "detritivore" condition, the inner (median) face bears several groups of superior lateral and inferior lateral setae (Figs. 6G,H; Q,R): These setae are presumably reduced or lost in the apomorphic or "raptorial" condition. One apomorphic condition of the pleustid propod is large and deep, the palm smooth, convex, and bearing a median tooth or cusp, and 1-2 groups of spines at the postero-distal angle (Figs. 6A,B; 6Q,R). Typically, the palm is lined submarginally on each side with a row of short setae. In another type of apomorphic condition (in strongly raptorial groups) the propod is very deep, the palm may be strongly toothed and/or incised, and the posterior angle armed with several groups of strong spines (Figs. 2I; 6J,K). In the latter instance, the posterior margin may become relatively short, and devoid of setae (or nearly so). In a third type of advanced condition, the propod becomes even more slender, and the palmar margin very oblique or merging imperceptively with the posterior margin (Figs. 6N,O,P).

The dactyl is usually large and strong, smoothly fitting the palmar margin (6J,K,M); its posterior margin is usually smooth, but may be serrated or dentate (Fig. 6P); here the palm is short and weak, the dactyl may exceed the spines at the palmar angle (Figs. 6A,B; 0,P).

Peraeopods 3-4

Typically slender, subequal (4 slightly shorter), with bases extending below the lower margins of all but the deepest coxal plates. Anterior and posterior margins of the basis are weakly (occasionally strongly) setose. The anterior and posterior margins of the distal segments (4-6) are typically spinose (Figs. 1A, F; 2K), rarely setose (Fig. 2L), or nearly bare (Fig. 1 H). Segment 5 is invariably shorter than 4 or 6, and is typically overhung proximally by the anterodistal process of segment 4 (Fig. 2P). The dactyl is usually strongly curved and powerful (Figs. 1 A, B; 2 I,L,P) but may be long and slender (Fig. 1 H), short and curved (Fig. 1 D,F), or short and minutely pectinate on the posterior margin (Fig. 2N).

Peraeopods 5-7

Primarily and classically homopodous. similar in form and size, although peraeopod 5 is usually the shortest, and peraeopod 6 slightly the longest (Figs. 1A,D,F; 2L). Rarely are they heteropodous, differing markedly in form and size (Fig. 1C). The coxae of peraeopods 5 & 6 are typically posterolobate and rounded behind (Figs. 3K,L) but may be angular both posteriorly and/or laterally (Fig. 3M - in Pleustinae). The anterior and posterior margins of distal segments (4-6) are usually spinose, with variations similar to those of peraeopods 3 and 4 noted above. Segment 5 is always shortest, and is variously overhung posteriorly by the postero-distal process of segment 4 (Figs. 1G; 2I). The dactyls are generally longer and stouter than those of peraeopods 3 and 4, except when short and pectinate on the anterior margin, as in the Dactylopleustinae (Fig. 2N).

Pleon plates 1-3

Generally deep and broad in form, the hind margins are usually smooth and the hind corners quadrate (Fig. 6C), acutely produced, hook-like (Figs, 1A,B; 2(O); 6I), or round and the hind margin serrated (Fig. 6F). Proximo-lateral cusps or teeth are present in some highly sculptured Pleustinae (Fig. 1E). The ventral margins, especially of plates 2 and 3, typically bear small spines, rarely setae (Fig. 6C).

Pleopods

All three pairs of pleopods are typically well developed and strongly natatory in both sexes. Pleopod 3 is slightly theshortest. The peduncles are long, nearly smooth or weakly setose laterally, and bear two serrated coupling spines (retinacula) on the medio-distal margin. The rami are long, subequal, multi-segmented, and richly plumose-setose. The inner margin of the proximal segments of the inner ramus are armed with 4-5 slender 'clothespin ' spines *(sensu* Barnard & Drummond, 1982). Within the Pleusymtinae, pleopod 2 is sexually dimorphic in one species *(Pleusymtes brachypalmus* Ishimaru, 1985) and pleopod 3 of a new genus and species from the North American Pacific coast is also sexually dimorphic.

Uropods

Uropods 1 and 2 are typically slender, with peduncle and both rami marginally and apically spinose (Figs. 1A, F; 2L,P). The peduncle of uropod 1 bears a disto-lateral ecdysial spine, best developed in the more advanced groups (Figs. 1A,B; 2X). The outer ramus of both uropods is shorter than the inner, often conspicuously so (Figs. 1B,G; 2P). Uropod 3 is shortest, the tips of the rami seldom extending beyond those of the other uropods. Both rami are longer than the peduncle. The outer ramus is usually distinctly shorter than the inner but may be subequal in some primitive species (within Atylopsinae, Austropleustinae).

Telson

The telson is typically plate-like, with an entire apical margin and a ventral mid-rib or keel. It varies in shape from short, subquadrate, even broadening distally, with a truncated apex (Fig. 3T), to elongate, tongue-like, or narrowing distally to a subacute apex (Figs. 3Q,S,U). In primitive groups, the apex may be cleft or incised, a situation that presumably represents incomplete fusion of the ancestral separated telson lobes (Figs. 3P,R). The apex bears paired notches, widely or narrowly separated, within each of which is based a small sensory seta or spine . The lateral margins and dorsal surface may bear small supernumerary setules, but true spines are lacking. Paired twin groups of sensory penicillate setae are located about midway dorsolaterally on each side; these may be slightly proximal (Fig. 3U) or distal (Figs. 3Q,T). The dorsal surface may be slightly hollowed or depressed.

The ventral keel of the telson is a feature almost unique to the Pleustidae. In most subfamilies it forms a deep, median, longitudinal rib, presumably of strengthening function. It is deepest centrally in Stenopleustinae and related subfamilies (Fig. 3W), but proximally in most others (Figs. 3V,X). In some primitive subfamilies (e.g. Atylopsinae), it may be shallow and weakly developed. It is lacking in Lafystiidae, Laphystiopsidae, and all groups relegated to the category of *Incertae Sedis.*

Coxal Gills

These are simple (unpleated or unlobed), sac-like or plate-like respiratory appendages attached to the posterior margin of the coxal segment of peraeopods 2-6. A small coxal gill may also be found on peraeopod 7 in a few primitive subfamilies (Atylopsinae, Austropleustinae (fide Just, Lincoln)) and in at least one species of Stenopleustinae. In most subfamilies, the gills are narrowly sac-like on peraeopods 2-4 but more broadly sac-like or plate-like on peraeopods 5-6. All gills are essentially narrowly saclike in primitive subfamilies (e.g. Atylopsinae, Eosymtinae and most Stenopleustinae) but are mainly broadly sac-like or plate-like in the others. The condition of the coxal gills of Pleustoidinae has not yet been noted or formally described.

Brood plates

Also known as oostegites, or brood lamellae, the brood plates are large, thin, lamellate structures attached to the hind margins of the coxal segments of peraeopods 2-5 of mature females. The first three pairs are large and broad, and the margins armed with numerous long simple brood setae. The fourth pair is typically smaller and broadly linear in form, the margins bearing relatively few setae.

Cuticle

Little is known of the surface microstructures of pleustid amphipods. No pleustids were formally included in the studies of Halcrow and Bousfield (1987), but unpublished authors' photographs reveal (in a species of Parapleustinae) regular surface polygons within which are irregular rows of micropores, and macropores; from some of the latter protrude prominent blade-like macrotrichs or microspines. Barnard (1964) has shown shallow pits and thickenings that cover the body of Mesopleustinae; these are common in many species within the Pleustinae (Bousfield and Hendrycks, in prep:, Part II).

SYSTEMATICS OF FAMILY PLEUSTIDAE

The family Pleustidae was initially defined by Stebbing (1906) and updated by Gurjanova (1951) and Barnard (1969a). These early diagnoses were relatively brief and encompassed about a dozen major character states, mainly of mouthparts, antennae, gnathopods, coxal plates, and general body form. The more recent diagnoses of Gurjanova (1972), Bousfield (1973, 1982a), and Lincoln (1979) encompassed a greater number of characters and character states that included features of gills, brood plates, and mouthparts not previously treated. The present diagnosis continues the trend towards increasingly broad coverage of morphological characters, and greater precision in treatment of character states. This format accommodates the much greater number and diversity of pleustid taxa revealed in this study, and more fully meets the requirements of numerical taxonomic methodology.

PLEUSTIDAE Buchholz, 1874

Paramphithoidae Sars, 1895 (partim): 343.
Pleustidae Stebbing, 1906: 870.—Barnard, 1969: 421.—Gurjanova, 1972: 634.—Bousfield, 1982a: 266.—Barnard & Karaman, 1991: 644.

Type Subfamily. Pleustinae Stebbing, 1906.

Subfamilies. Atylopsinae, new subfamily [p. 34]; Stenopleustinae, new subfamily [p. 35]; Austropleustinae, new subfamily [p. 34]; Mesopleustinae, new subfamily [p. 36]; Pleustoidinae, new subfamily [p. 37]; Eosymtinae, new subfamily [p. 37]; Pleusymptinae, new subfamily [p. 37]; Dactylopleustinae, new subfamily [p.38]; Pleustinae, new subfamily (p. 39]; Pleusirinae, new subfamily [p.39]; Neopleustinae, new subfamily [p. 40]; and Parapleustinae, new subfamily [p. 41].

Diagnosis. Body small to medium large, often broadened anteriorly, usually toothed or carinated dorsally, especially on the pleon; surface often strikingly coloured or maculated. Urosome 2 short, often dorsally occluded by segments 1 and 3. Head deep, variously (often strongly) rostrate; anterior head lobe pronounced, acute or rounded. rarely incised; inferior antennal sinus distinct, inferior lobe acute, or produced. Eyes typically large, well pigmented. subrotund to subrectangular. Antennae short to medium-long, slender, lacking calceoli. Antenna 1 longer than 2, peduncular segment 1 large, often produced distally; segments 2 and 3 often short; accessory flagellum minute or lacking. Buccal mass shallow to medium deep, regressed slightly behind head.

Upper lip apically notched or incised; lobes usually asymmetrical; epistome with rounded median anterior ridge. Lower lip, inner lobes varying from tall and narrow to broad and squat; outer lobes: from large and closely approximated to small, rounded and widely separated.

Mandible well developed. Molar present, basically with strong, apical, triturating surface, secondarily reduced, setulose or smooth, non-triturative. Spine-row strong, blades often thickened, pectinate, blade-like, or "molarized" (p. 29). Left lacinia multi-dentate (6-12+ teeth); right lacinia present in primitive subfamilies, lacking in advanced groups; incisor strongly toothed. Maxilla 1, inner plate small, with few (0-4) apical setae; outer plate with 9 (6-17) tall pectinate spines; palp large, 2-segmented, apically spinose and setose. Maxilla 2, inner plate shorter, often broader than outer, lacking facial row of setae, but inner margin usually with 1-2 large plumose setae. Maxilliped strongly developed; outer plate basically large, with convex outer margin, secondarily reduced, slender, columnar in form;inner plate often short, apex subtruncate, bearing setae and spines of large or small types , inner margin with masticatory setae or spines; palp large, semi-raptorial, segment 2 largest, segment 3 often produced apically beyond base of slender dactyl.

Coxae 1-4 usually large, deeper than corresponding peraeonal plates, increasing posteriorly; mid-point of hind margins occasionaly weakly processiferous; lower hind corner usually with small cusp(s); coxa 1 often short, modified; coxa 4 excavate behind.

Gnathopods 1 and 2 variously (often strongly) subchelate, occasionally simple, usually subsimilar (2 larger), occasionally sexually dimorphic; palm often with median tooth, postero-distal angle with stout spine cluster(s); carpus not longer than propod, hind lobe often narrow, deep; basis with setose anterior margin; dactyls with short unguis.

Peraeopods 3-7 normal, little modified, segments spinose, rarely setose, dactyls strong. Peraeopods 3 and 4 subequal (3 longer). Peraeopods 5-7 regularly homopodous (similar in size and form); coxae postero-lobate, usually rounded behind, occasionally ridged laterally; bases expanded, rounded behind, not distally narrowing, segment 4 variously overhanging shorter segment 5 behind.

Pleon side plates large, overlapping, hind corners usually acuminate, hind margin smooth or serrated. Pleopods large. Uropod 3, rami lanceolate, margins spinose (lacking plumose setae), inner ramus the longer, both rami longer than peduncle. Telson short to medium, with mid-ventral keel; margins smooth or setulose (not spinose); apex variously rounded, rarely incised.

Coxal gills primarily small and sac-like, secondarily large and plate-like, on peraeopods 2-6, rarely on peraeopod 7.

Brood plates on peraeopods 2-4 large, broad, on 5 small, margins with numerous simple setae.

Mature male typically smaller than mature female.

Taxonomic Commentary. Bousfield (1979, 1982a, 1983) established superfamily Leucothoidea to encompass the Pleustidae and other deep-plated, mostly smooth-bodied, micro-carnivorous, benthic inquilines and commensals, of fully marine environments. All have variously reduced or modified mouth-parts, non-glandular, prehensile, weakly ambulatory peraeopods with postero-lobate coxae 5-7; lanceolate, non-foliaceous uropod rami; and short, plate-like (usually keeled) telsons.

Originally included in the superfamily were the Pleustidae, Laphystiopsidae, Amphilochidae, Leucothoidae, Anamixidae, Maxillipiidae, Colomastigidae, Pagetinidae, Nihotungidae, Tulearidae, Stenothoidae, Thaumatelsonidae, and Cressidae. Subsequently, the family Colomastigidae was transferred to the Liljeborgioidea (near Sebidae - see Barnard, 1971); the Anamixidae was found to consist entirely of males of the genus *Leucothoides,* and may require submergence within Leucothoidae (see Thomas and Barnard, 1983). The status of Laphystiopsidae is uncertain; it is proving closely related to Lafystiidae, now transferred from superfamily Stegocephaloidea to the Leucothoidea (Bousfield, 1992).

In most character states, however, the Pleustidae appears to be the most plesiomorphic of all leucothoidean families and the most closely related, through a series of intermediate, isolated genera, to the superfamily Eusiroidea (see below; Shaw, personal comunic). In this regard, pleustid genera had originally been placed within the Paramphithoidae, one of the most advanced families of superfamily Eusiroidea, by Sars (1895) and earlier authors. However, despite these clinal linkages, the present study confirms the correctness of Stebbing's original decision (1906) to give formal recognition to this assemblage as a fully distinctive family, the Pleustidae.

Biogeographic commentary. The family Pleustidae consists of two main distributional entities, each of which exhibits strong internal taxonomic and phyletic relationships. One group (consisting of most subfamilies) is essentially Holarctic in distribution; its strongest diversity is centred in the North Pacific with its most primitive member confined to the deep sea (p. 53). By contrast, members of the group comprising the Atylopsinae, Austropleustinae, and Stenopleustinae, are mainly austral or confined to the North Atlantic and adjacent Arctic region. Of these, subfamily Stenopleustinae is most like some advanced northern subfamilies. However, some of the apparent similarities are homoplasious (p. 52). Evolutionary processes within family Pleustidae appear to be very complex and still not fully understood.

SUBFAMILIES OF PLEUSTIDAE

ATYLOPSINAE, new subfamily

Calliopiidae Stebbing, 1906: 299 (partim).—J. L. Barnard 1969a: 167.
Eusiridae H. G. Andres, 1986.—Barnard & Karaman, 1991: 284.

Type genus. *Atylopsis* Stebbing, 1888: 294.—Barnard & Karaman, 1991: 308. (Type species - *Atylopsis emarginatus* Stebbing, 1888).

(CONT'D ON P. 34)

KEY TO SUBFAMILIES OF PLEUSTIDAE

1. Coxal gill present on peraeopod 7 in some or all members; maxilliped palp segment 3, apex oblique, more or less produced beyond base of dactyl (Fig.S K); dactyl slender, non-pectinate (Fig. 5 K) or weak or lacking (Fig. 5 M); pleon plate 3 often rounded and/or serrated behind (Figs. 2m; 6 F); telson keeled keeled centrally (Fig. 3 W), often cleft or notched apically . . . . 2.

—Coxal gill lacking on peraeopod 7; maxilliped palp segment 3 apically truncate or rounded (Fig. 5 L), if oblique and produced, dactyl is straight, pectinate [Fig. 5 (1)]; pleon plate 3 subquadrate, hind corner usually acuminate or produced, hind margin not serrated (Figs. 6 C, 1): telson keeled proximally (Fig. U. V, X), or if centrally, rostrum elongate (Fig. 3 B)A, B) . . . . 4.

2. Upper lip with shallow notch, lobes subsymmetrical (Figs. 4A,B)); lower lip, inner lobes small, narrow, outer lobes large, little separated (Fig. 4I); maxilla 2 inner plate with 2-3 stout facial setae; mandibular blades slender, weakly pectinate (Fig. 5A) . . . . **Atylopsinae** (p. 34).

—Upper lip deeply notched, lobes asymmetrical (Fig. 4 E); lower lip, inner lobes large, wide, outer lobes small, widely separated (Figs. 4 L,M); maxilla 2, inner plate lacking stout marginal plumose setae; mandibular blades short, pectinate (Fig. 5 H) . . . . 3.

3. Gnathopods weakly subchelate or simple, subequal IFigs. 6 A, B; 6(0), P); carpus and propod elongate, palm of propod , median tooth lacking; telson often apically cleft . . . . **Austropleustinae** (p. 34)

—Gnathopods often strongly subchelate, rarely subequal (2 larger. often of different form) (Figs. 6 G, H); carpus of gnathopod 2 not elongate, deep (Figs. 6 J, M), palm of propod with median tooth (Figs. 6 Q, R); apex of telson entire (Fig. 3S) . . . . **Stenopleustinae** (p. 35)

4. Mandibular molar normal, with strongly triturative apex (Figs. 5 A-D); coxa 1 bent forwards distally, apex often acute (Fig. 2P); antenna 1, peduncular segment 1 often with acute distal process (Figs. 40, P) 5.

—Molar reduced, apex smooth or setulose, non-triturative (Figs.4 E, F); coxa 1 normal, not bent forwards distally (Fig. 1 D, 2 L); antenna 1, peduncular segment 1 not produced distally as acute process . . . . 8.

5. Mandibular right lacinia present, blade-like (Fig.S D); left lacinia with few (6-8) teeth (Fig. 5 A, C, D); urosome segment 2 not occluded dorsally (Fig. 7); maxilliped, outer plate broad, outer margin convex (Figs. 5 L, O); lower lip, inner lobes narrow, deep. (Figs. 4 H, I, J) . . . . 6.

—Right lacinia lacking; left lacinia with many (8+) teeth; urosome 2 occluded dorsally (or nearly so); maxilliped outer plate narrow, columnar (Figs.S J, N); lower lip, inner lobes squat, wide (Fig. 6 N) . . . . **Pleusymtinae** (p. 37)

6. Telson keeled proximally (Figs. 3 V, X); rostrum medium extending little beyond lateral head lobe (Figs. 3 E; 7); mandibular molar medium, apex with triturative ridges marginally only (Figs. 5 C,D); gnathopods subsimilar in form and size; palm of propod lacking median tooth (Figs.6 A, B; 6 J,K) . . 7.

—Telson keeled centrally (Fig. 3 W); rostrum strong, extending well beyond lateral head lobe (Fig. 2 P); mandibular molar strong, apex with full triturative ridges (Fig. 5A); gnathopods strongly dissimilar in form and size (Figs.6G, H); propod palms with median tooth . . . . **Mesopleustinae** 36)

7. Body medium to large, mid-dorsally and dorso-laterally ridged or carinated (Fig. 2O); gnathopods "melphidippoidean" in form (lower margin of carpus straight); antenna 1, peduncle 1 distally truncate, unproduced . . . . **Pleustoidinae** (p. 37)

—Body small, smooth above (Fig. 7); gnathopods ordinary, carpal lobe rounded below (Fig.7 detail); antenna 1, peduncle 1 usually with acutely produced distal process (Figs. 7 detail; 4O,P). . **Eosymtinae** (p. 37)

Key to Subfamilies (cont'd)

8. Gnathopod propods lacking median palmer tooth; upper and lower lips of intermediate type (Figs. A D; 4K, L); uropod 1 with strong disto-lateral peduncular spine . . . . 9.
—Gnathopod propods with median palmar tooth; upper and lower lips of advanced type (Figs. 4E-G; 4M, N); uropod 1 with strong disto-lateral penduncular spine . . . . 11.

9. Body strongly carinated (Figs. 1 E, F); rostrum strongly developed (Figs. 3A-C); mandibular molar reduced to stub, setulose (Fig. 5 F); mandibular palp segment 3 usually with many (5+) basal "A" setae . . . . **Pleustinae** (p. 39)
—Body smooth above; rostrum little exceeding lateral head lobe (Figs. 3 D, E); mandibular molar inflated, apex smooth (Fig, SE); mandibular palp segment 3 lacking basal "A" setae . . . . 10.

10. Urosome 2 dorsally occluded (or nearly so) (Fig. 10); peraeopod dactyls normal, simple; gnathopods powerfully subchelate, "eusiroidean" in form (Figs. 6 D, E); uropod I with weak disto-lateral spine . . . . **Pleusirinae** (p. 39)
—Urosome 2 not occluded dorsally (Fig. 2N); peraeopod dactyls small, inner surface finely crenulated; gnathopods weakly subchelate, propod and dactyl elongate, shallow (Figs .6 A, B); uropod 1 lacking disto- lateral peduncular spine . . . . **Dactylopleustinae** (p. 38)

11. Body usually dorsally carinate or mucronate, especially on pleon (Fig. 2 (I)); rostrum medium, extending beyond lateral head lobe (Fig. 2M); mandibular blades normal, slender; urosome 2 not fully occluded dorsally; coxae 1-3, lower hind cusps strong (Figs. 3G, H . . . . **Neopleustinae** (p. 40)

—Body dorsally smooth; rostrum short, not extending beyond lateral head lobe (Fig. 3 D); mandibular blades often strongly thickened or molarized (Fig. 5 F); urosome 2 dorsally occluded; coxae 1-3, hind cusps very weak or lacking (Fig. 3 J) . . . . **Parapleustinae** (p. 41)

(ATYLOPSINAE - CONT'D FROM P. 32))

Genera. One new genus based on *Pleustoides mediterraneus* Ledoyer, 1986; to be described (Bousfield & Hendrycks, in prep., Part III).

Diagnosis: Body smooth or dorsally mucronate. Urosome 2 not dorsally occluded. Antennae slender; antenna 1, peduncular segments 2 and 3 short; basal flagellar segments weakly conjoint, possibly callynophorate (*sensu* Lowry, 1986). Accessory flagellum minute.

Upper lip, median notch shallow, lobes subsymmetrical. Lower lip, inner lobes small, outer lobes large, little separated. Mandible, molar large, triturating surface fully ridged, medial marginal plumose, flagellum strong; left lacinia 5-6 dentate; right lacinia present, tricuspate or chisel-like; blades of spine row slender, weakly pectinate; palp segment 2 widened, segment 3 basally with 1-2 "A" setae. Maxilla 1, outer plate with 9-11 apical spines; inner plate with 1-4 apical seta(e); palp segment 1 narrow, segment 2, subapically setulose. Maxilla 2, inner plate little expanded, with 2-3 stout facial setae. Maxilliped, outer plate large, medially broadest and convex; inner plate tall, apex with "button" spines; palp segment 3, apex oblique, typically extending beyond base of smooth, slender dactyl.

Coxal plates 1-4 shallow, 4th weakly excavate behind, lower hind corners lacking cusps. Gnathopods slender, weakly subchelate or simple; carpus and propod slender, hind margins shallow, setose; palmer margin lacking median tooth; dactyls often serrate.

Peraeopods 3-7 slender, segment 4 little overhanging segment 5 proximally, dactyls slender. Peraeopods 5 to 7 homopodous or heteropodous, 7 longest.

Pleon plates 1-3, hind corners, obtuse or subquadrate, little produced. Uropods 1 and 2 slender; uropod 1 lacking latero-distal peduncular spine. Uropod 3, rami slender, elongate, subequal or unequal.

Telson apically cleft, notched, or entire; keel not described in any species (weakly present?).

Coxal gills on peraeopods 2-7 slender, sac-like. Brood plates large, broad on peraeopods 2-4, smaller on peraeopod 5 (Stebbing, 1888).

Taxonomic Commentary. The plesiomorphic character states are best retained in species of *Atylopsis. "Pleustoides" mediterraneus* Ledoyer, 1986, appears to consist of two species, both in a genus distinct from *Pleustoides* Gurjanova, 1972. The genus is to be described elsewhere (Bousfield and Hendrycks, in prep., Part III). Although not quite complying with the typical form of the maxilliped palp, peraeopods 5-7, and telson, the generic group is provisionally placed within the Atylopsinae until the types can be fully redescribed.

AUSTROPLEUSTINAE, new subfamily

Type Genus. *Austropleustes* K.H Barnard, 1931: 428. (TYPE species - *A. cuspidatus* K.H Barnard, 1931: 428).

Genera. *Tepidopleustes* Karaman & Barnard, 1979: 113. (TYPE species - T. *barnardi* [Ledoyer, 1972]: 262).

Diagnosis. Body small to medium. Pleon and posterior peraeonal segments toothed dorsally. Urosome 2 not occluded dorsally. Rostrum medium, slightly exceeding lateral headlobe, weakly keeled. Eyes large, subtriangular or rhomboidal. Antennae long, slender; antennae 1, peduncular segments 2 and 3 short; accessory flagellum very small but distinct, 1-segmented (fide Lincoln).

Upper lip deeply notched; lobes asymmetrical. Lower lip, inner lobes shallow, wide; outer lobes oblique, rounded.

Mandible, molar reduced, apex with small grinding surface or minutely spinulose and setulose; spine-row short to medium, with 3-12 slightly modified blades; left lacinia normally 8-12 dentate; right lacinia present, bidentate (multicuspate - fide Lincoln); palp segment 3 with 2 basal "A" setae segment 2 weakly setose. Maxilla 1, outer plate with 9 apical spines; inner plate with single apical seta; palp slender . Maxilla 2, inner plate not broadened, lacking inner submarginal plumose seta(e). Maxilliped outer plate widest basally, outer margin convex distally, inner margin setose; inner plate short, apex with few "button" spines; palp segment 3 elongate, apex oblique, produced beyond base of slender, non-pectinate dactyl that may be reduced or lacking.

Coxal plates 1-4 small, shallow, regularly increasing, not covering leg bases; lower margins rounded, hind cusp small or lacking, Gnathopods weakly subchelate or simple, subsimilar in form and size, (not sexually dimorphic?); bases weakly setose antero-distally; carpus shallow, elongate (>1/2 propod); propod shallow, palm short, oblique, lacking median tooth, hind margin setose.

Peraeopods 3-7 slender; segment 6 longest, 4 weakly overhanging 5, dactyls strong. Peraeopods 5-7 variably heteropodous, longest posteriorly; bases somewhat dissimilar in size and form, lobate.

Pleon plates subquadrate or rounded behind, posterior marginfinelyserrate. Uropods 1 and 2, outer ramus distinctly the shorter; uropod 1 with disto-lateral peduncular spine usually lacking. Uropod 3, outer ramus variably shorter than inner; peduncle may be produced distally beneath inner ramus. Telson short, apically cleft or rounded, keeled centrally.

Coxal gills on peraeopods 2-7, small, sac-like. Brood plates undescribed.

Taxonomic Commentary. Despite some plesiomorphic character states, subfamily Austropleustinae consistently clusters with the advanced pleustid subfamilies (p. 88). Its closest affinities are with the Stenopleustinae, linked via the genus *Arctopleustes,* especially in the rounded coxal plates, produced form of the maxilliped palp, and slender, nonpectinate dactyl, rounded and serrated pleon plates, and centrally keeled telson. Within subfamily Austropleustinae, the genus *Tepidopleustes* is distinguished by its reduced maxillipedal dactyl and by the lack of a distal peduncular process on uropod 3.

STENOPLEUSTINAE, new subfamily

Type Genus. *Stenopleustes* Sars, 1895: 354. (TYPE species - *S. malmgreni* (Boeck, 1871).

Genera. *Sympleustes* Stebbing, 1899: 209. (TYPE species - *S. latipes* (M. Sars, 1858); *Arctopleustes* Gurjanova, 1972. (TYPE species - *A. rasmyslovi* (Gurjanova, 1951). Two other genera, one based on *Sympleustes olriki* Hansen, 1887, and the other on *Stenopleustes gracilis* Holmes, 1905, to be described (Bousfield & Hendrycks, part III, in prep.).

Diagnosis. Body small to medium, pleon occasionally dorsally mucronate or toothed. Urosome 2 not occluded dorsally. Rostrum medium (p. 19). Anterior head lobe acute or subacute, rarely notched. Eyes large, subrectangular. Antennae slender, elongate:antenna 1, basal flagellar segments often conjoint; peduncular segment 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip, inner lobes shallow; outer lobes moderately separated, oblique. Mandible, molar weakly to strongly triturative, narrowing distally and/or compressed, grinding surface with "cobbled" core and marginal ridges or projecting teeth; spine-row short, blades normal or thickened and pectinate, inter-blade setae numerous; left lacinia multi-dentate (8+ teeth); right lacinia present, but reduced blade-like, or vestigial; palp large, segment 3 often lacking "A" setae. Maxilla 1, outer plate with 6-7 apical spines; inner plate with 1(0-3) apical seta; palp normal. Maxilla 2, inner plate narrow, lacking marginal plumose seta(e). Maxilliped, outer plate medium, broadest basally, distal outer margin and apex convex, inner margin of a cutting type, scalloped or indented in one genus; inner plate medium, apex with "button" spines; palp segment 3, apex oblique, extended acutely beyond base of slender, non-pectinate dactyl.

Coxae 1-4 medium deep, lower margins rounded, weakly (or not) cusped behind; coxa 1 normal or expanded distally. Gnathopods of three main types: (1) subsimilar, slender, weakly to moderately subchelate, carpus and propod shallow (*Stenopleustes* type), (2) strongly subchelate, but dissimilar in size (*Sympleustes* type) and (3) grossly dissimilar in size and form, gnathopod 1 weakly subchelate (*Arctopleustes* type). In all three types the bases are setose anteriorly; the merus has an acute postero-distal process, the carpus of gnathopod 1 is elongate (>2/3 propod); the propod palm has a median tooth; and the posterior margin is setose.

Peraeopods 3-7 slender to strong, dactyls slender. Peraeopods 5-7 homopodous; coxae deep; bases broad;

segment 4 often strongly overhanging 5; dactyls distinctly larger than in peraeopods 3 & 4.

Pleon plates normal, hind corner acuminate, hind margins smooth or serrated. Uropods 1 and 2 long; uropod 1, rami subequal, latero-distal peduncular spine small or lacking. Uropod 3, rami long unequal. Telson rounded behind, keeled centrally.

Coxal gills on peraeopods 2-6, occasionally on peraeopod 7, small, sac-like. Brood plates large, broad.

Taxonomic commentary. This medium-sized subfamily (about a dozen species in 5 genera) is marginally included in the advanced group of subfamilies (p. 45). Members retain several important plesiomorphic traits, notably the triturative molar, the right lacinia, the convex form of the maxilliped outer plate, the conjoint proximal flagellar segments of antenna 1, the unoccluded urosome 2, and the sac-like coxal gills, present on peraeopod 7 in one genus. The subfamily is closely related to the Austropleustinae (p. 51), yet apparently shares an atylopsinid ancestry (p. 52). Stenopleustinids also share some characteristics with neopleustinids but the form of the maxilliped palp is apparently convergent.

Biogeographical commentary. Members of all five genera are restricted to intermediate shelf waters of the North Atlantic and adjacent Arctic regions. One species (of the most southerly genus) also occurs off the coast of California.

MESOPLEUSTINAE, new subfamily

Pleustidae Stebbing, 1906 (partim): 315.—Gurjanova, 1951 (partim): 634.—Barnard, 1969a (partim): 422.—Barnard & Karaman, 1991 (partim): 648.

Type genus. *Mesopleustes* Stebbing, 1899: 209. (TYPE species - M. *abyssorum* [Stebbing, 1888].

Diagnosis. Body robust, weakly carinated. Urosome 2 not occluded dorsally. Rostrum strong. Antenna 1, peduncular segments 2 and 3 elongate. Accessory flagellum minute. Eyes unpigmented.

Upper lip shallowly notched, lobes weakly asymmetrical. Lower lip, inner lobes indistinct; outer lobes large, little separated. Mandibular molar strong, triturating surface fully ridged, medial marginal plumose setae present; distal molar process or hump weak; blades of spine-row simple; left lacinia 6-dentate, right lacinia present, bifid; palp medium, segment 3 lacking "A" setae. Maxilla 1, outer plate with 10-11 apical spine-teeth; inner plate with 4 apical setae; palp segment 1 with lateral wing-like process. Maxilla 2, inner plate not expanded, with 1 (normally) submarginal plumose setae. Maxilliped, outer plate large, broadest medially, with convex outer margin; inner plate tall, with 3-6 apical spines; palp segment 3, apex subtruncate, not produced beyond pectinate dactyl.

Coxae 1-3 narrow, deep, hind corners with cusps; coxa 1 sharply bent forward distally. Gnathopods strongly subchelate, dissimilar in size and form (2 larger); bases setose anteriorly; carpus short, deep; propod posterior margin strongly setose and/or spinose, palmar margin with proximo-median tooth, that of gnathopod 2 medially excavate.

Peraeopods 3-7 stout, spinose; bases of 5-7 with strong postero-distal lobes; segment 5 short, strongly overhung proximally by segment 4; dactyls strong.

Pleonal plates, hind corners acuminate, hind margins smooth. Uropods 1 and 2 strong, spinose; uropod 1 lacking disto-lateral peduncular spine. Uropod 3, outer ramus distinctly the shorter. Telson short, keeled centrally, apex weakly incised or entire, penicillate setae distally inserted.

Coxal gills plate-like, on peraeopods 2-6, lacking on P7. Brood plates unknown.

Taxonomic commentary. This monotypic group retains a number of plesiomorphic character traits including the elongate peduncular segments of antenna 1, complete triturating molar ridges and plumose flagellum, 6-dentate left lacinia and bifid right lacinia, 11 apical spines of maxilla 1 outer plate; and broad maxilliped outer plate and of Pleustoidinae (see phenogram and cladogram (pp. 51-52). However, its advanced character states, including the form of coxa 1, gnathopods, uropod 3, telson, and coxal gills combine some features of both the Pleusymtinae and Stenopleustinae.

Distributional Commentary. Abyssal; mainly Indo-Pacific. A phyletic and biogeographically relict group.

PLEUSTOIDINAE, new subfamily

Type Genus. *Pleustoides* Gurjanova, 1972: 134. (TYPE species - P. *carinatus* Gurjanova, 1972).

Diagnosis. Body dorsally and laterally carinated. Urosome 2 not occluded above. Rostrum short. Eyes reniform. Antennae slender; antenna 1, segment 3 short. Accessory flagellum unknown.

Upper and lower lips not described but presumed plesiomorphic. Mandibular molar strong, grinding surfce with smooth central core and radiating ring of triturating ridges; plumose flagellum not described (probably present?); spine row short, blades slender; left lacinia 6-7 dentate?; right lacinia bifid, blade-like (?); palp segment 3 apparently with one basal "A" seta; posterior marginal setae elongate. Maxilla 1, outer plate with 9 apical spines(?); inner plate with 1-2 apical plumose setae; palp broad, outer margin setose. Maxilla 2, inner plate small, little broadened, with 2(3) submarginal plumose setae. Maxilliped, outer plate large, broadest proximally, outer margin convex distally, inner margin spinose; inner plate tall, apex with stout spines; palp segment 2 elongate, segment 3, apex rounded, unproduced.

Coxae 1-4 medium deep, lower margins straight; coxa 1 distally bent forward, subacute. Gnathopods of "melphidippoidean" type (i.e. strongly subchelate, closely subequal, carpus and propod elongate, carpus with shallow, straight, setose hind lobe, propod palm oblique, untoothed, exceeded by dactyl); basis weakly to moderately setose anteriorly.

Peraeopods strong, segments elongate, segment 4 strongly overhanging segment 5. Peraeopods 5-7, bases slightly heteropodous, increasing posteriorly. Dactyls not described.

Pleon plates deep, broad, hind corners acute, hind margin smooth. Uropods I and 2, rami elongate, unequal; uropod 1 apparently lacking disto-lateral peduncular spine. Uropod 3, rami slender, unequal. Telson elongate, notched apically, keeled proximally.

Coxal gills and brood plates undescribed.

Taxonomic commentary. Although original material has not been re-examined, Gurjanova' s descriptions and figures of species of *Pleustoides* suggest a unique genotype that cannot be placed within the other 11 subfamilies here described. No other subfamily group exhibits the combination of dorso-laterally ridged or carinated body, small rostrum, elongate maxilliped palp, short basal segment of the maxilliped outer plate, and "melphidippoidean" gnathopod. As far as can be determined, features of the mouthparts are basically plesiomorphic (Table I) and ally it most closely with subfamilies Eosymtinae and Mesopleustinae.

As noted elsewhere (p. 33), the Mediterranean genus *Pleustoides* of Ledoyer (1986) differs from Gurjanova's western Pacific genus in several major character states, notably the heteropodous condition of the peraeopods, form of the gnathopods, and various peculiarities of the mouthparts. Ledoyer' s form is tentatively given new generic status within subfamily Atylopsinae.

EOSYMTINAE, new subfamily

Type Genus. *Eosymtes,* new genus [p. 43]. (TYPE Species - *Eosymtes minutus,* new species [p. 43].

Genera. One additional new genus and new species, to be described in Bousfield & Hendrycks, Part IV, in prep.

Diagnosis. Small, smooth-bodied, pleustids exhibiting mainly plesiomorphic character states. Urosome 2 not dorsally occluded. Rostrum medium. Anterior head lobe rounded to subacute; inferior sinus shallow to medium deep. Eye medium, reniform or round. Antenna 1 slender, flagellar segments few (10-17); peduncle 1 distally processiferous, segments 2 & 3 not markedly reduced. Accessory flagellum minute.

Buccal mass shallow, regressed beneath head. Upper lip shallowly notched, lobes weakly asymmetrical. Lower lip, inner lobes narrow; outer lobes large, not widely separated. Mandible, molar strong, triturative face with smooth core and peripheral ridges or teeth, medio-distal plumose flagellum, and distal medial hump; spine-row short, blades acute, distally pectinate; left lacinia 6-8 dentate, right lacinia present, bifid, blade-like; incisor irregularly dentate; palp medium, slender; segment 3 with single basal "A" seta, and simple or weakly pectinate distal marginal setae. Maxilla 1, inner plate with 12 apical plumose setae; outer plate with 9 apical spines; palp slender, segment 1 regular. Maxilla 2, inner plate slightly broadened, submarginally with 2 stout plumose setaea. Maxilliped, outer plate medially widest and convex; inner plate tall, apex with outer slender spines and inner stout spines; palp slender, segment 2 longest, segment 3, apex rounded, not produced distally.

Coxal plates 1-3 medium shallow, hind corners cuspate; coxa 1 shortest, distally bent forwards. Gnathopods strongly subchelate subequal (2 larger); margins of bases nearly bare; carpus medium short, hind lobe deep; propod longer than carpus; palmar margin smooth, convex, lacking median tooth, hind margin bare.

Peraeopods 3-7 slender, segment 4 weakly overhanging 5; dactyls elongate. Peraeopods 5-7 basically homopodous, coxae medium to deep, posterolobate; bases broad, subsimilar.

Pleon plates broad, hind corners square or acuminate. Pleopod 3, outer margin of peduncle setose. Uropods 1 and 2 slender, rami narrow, unequal to subequal; uropod 1 with a small disto-lateral peduncular spine. Uropod 3, rami markedly unequal. Telson medium long, apex slightly incised or entire; keeled proximally.

Coxal gills on peraeopods 2-6, small, slender, sac-like. Brood plates 2-5 broad, deep, margins with few long setae.

Etymology. From the Greek root *"Eo"* (dawn or early) and *"symtes"* (suffix of *pleusymtes*), in reference to its plesiomorphic character states, many of which appear ancestral to those of subfamily Pleusymtinae.

Taxonomic commentary. This small generic grouping is readily placed within the primitive group of pleustid subfamilies, close to Mesopleustinae and Pleustoidinae (p. 36). Many of its features e.g. of antennal peduncle, mouthparts, coxal plates, uropods, and telson would seem antecedent to subfamily Pleusymtinae of the advanced subgroup of families within Pleustidae (Table II, Fig. 9).

PLEUSYMTINAE, new subfamily

Type Genus. *Pleusymtes* Barnard, 1969a: 425. (TYPE species *Pleusymtes glaber* (Boeck, 1861).

Genera. *Pleustomesus* Gurjanova, 1972. [TYPE species - *Pleustomesus medius* (Goes, 1866). Six new genera, mostly monotypic, are to be described in Bousfield and Hendrycks, Part IV, in prep. One genus is based on *Incisocalliope karstensi* Barnard, 1959a (Arctic); another on *Pleusymtes coquillus* Barnard, 1971 (North Pacific); and the other four genera on new species from the western North Pacific shelf region.

Diagnosis. Body small to medium, slender, dorsally smooth, rarely toothed. Urosome 2 dorsally occluded (or nearly so). Rostrum short (rarely long). Anterior head lobe typically acute; inferior sinus produced acutely below antenna 2. Eye large, subrotund or rhomboidal. Antennae slender; antenna 1, peduncular segment 1 elongate and distally processiferous; segments 2 and 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip squat, inner lobes shallow, wide, outer lobes oblique, rounded. Mandible, molar strong, triturating surface nearly smooth (rarely pebbled), pavement-like, margins sharp, even; blades of spine row few (5-10), stout, pectinate, distal blade(s) occasionally chisel-shaped; left lacinia 6-11 dentate, right lacinia lacking; palp slender, segment 3 with single basal "A" seta. Maxilla 1, outer plate with 9 apical spines; inner plate small, with 1 (rarely 2) apical seta; palp medium to broad, segment 1 with weak outer marginal lobe and seta(e). Maxilla 2, inner plate broadened, with single marginal plumose seta. Maxilliped, outer plate broadest basally, outer margin curved distally, apex subtruncate, slender-spinose; inner plate short, apex with "button spines", inner marginal setae numerous (4-9). Palp segment 3 apically rounded or truncate, not produced; dactyl long, micropectinate.

Coxal plates 1-4 large, covering leg bases, increasing posteriorly, subquadrate below, hind corners of 1-3 cuspate; coxa 1 distinctly smallest, distally narrowing and often bent forward. Gnathopods relatively strongly subchelate, subequal, weakly sexually dimorphic; bases variously setose anteriorly; merus (segment 4) with acute postero-distal process; carpus usually short, hind lobe deep; propod as deep as carpus, median palmar tooth small (rarely lacking); hind margin short, weakly setose, or bare.

Peraeopods 3-7 generally slender; segment 4 distinctly overhanging 5; dactyls slender, long. Peraeopods 5-7 homopodous; coxae deep, bases broad, lobate behind.

Pleon plates deep, hind corners usually acuminate, produced, or upturned, hook-like, hind margins smooth. Pleopod 2 or 3 may be sexually dimorphic. Uropods 1 & 2 slender, spinose; rami of uropod 1 subequal or unequal; uropod 1 with a strong disto-lateral peduncular spine. Uropod 3, rami unequal, narrow, spinose. Telson rounded or subacute apically, keeled proximally.

Coxal gills large, sac-like on peraeopods 2 & 3, plate-like on peraeopods 4-6. Brood plates normal.

Taxonomic Commentury. This large subfamily (about 30 species in 8 genera, half in *Pleusymtes*) is clearly a member of the advanced group of subfamilies (p. 47), although several important character states (e.g. of mandibular molar, maxilliped outer plate) are intermediate. Its immediate ancestry within the group of primitive subfamilies would seem closest to the Eosymtinae, with which it shares a number of similarities of the antennae, mouthparts, coxal plates, peraeopods, and telson.

Biogeographical Commentary. Of the eight genera within subfamily Pleusymtinae, five are endemic to the North Pacific region. The other three genera (especially *Pleusymtes*), containing most of the species, are mainly arctic and subarctic, penetrating southwards mainly in the North Atlantic region.

DACTYLOPLEUSTINAE, new subfamily

Pleustidae Barnard & Karaman, 1991 (partim): 544.

Type Genus. *Dactylopleustes* Karaman & Barnard, 1979: 112. (TYPE species - *Parapleustes echinoicus* Tzvetkova, 1975, original designation.)

Diagnosis. Body small, smooth, deep-plated. Urosome 2 not dorsally occluded. Rostrum medium. Lateral head lobe rounded. Eyes reniform. Antennae short, subequal, subpediform; antenna 1, peduncular segments 2 and 3 short. Accessory flagellum lacking.

Upper lip shallowly notched, lobes weakly asymmetrical. Lower lip, inner lobes deep, outer lobes oblique. Mandible, molar large, inflated, apical surface non-triturative; blades of spine-row slender, unmodified; left lacinia 6-7 dentate, right lacinia lacking; palp slender, segment 3 lacking "A" setae. Maxilla 1, outer plate short, broad, apical spines 9-16, variable in type; inner plate with one apical seta; palp broad, segment 1 large. Maxilla 2, plates little broadened, outer plate with strong apical spines; inner with 1 marginal plumose seta. Maxilliped, outer plate narrow, basally broadest, outer margin distally convex, inner margin concave; inner plate short, apex oblique, with 1-2 "button" spines; palp segment 2 short; segment 3 distally rounded.

Coxae 1-4 deep, covering leg bases; lower margins quadrate, with multiple hind cusps; coxa 1 distinctly the shortest. Gnathopods small, slender, weakly subchelate; basis setose anteriorly; carpus elongate (= propod), lobe shallow; propod palm short, smooth, hind margin setose; dactyl short, stout, overlapping palm.

Peraeopods 3-7 short, margins finely spinose; dactyls short, inner margins finely crenulate or pectinate. Peraeopods 5-7 homopodous but trending to heteropody in one species; coxae very deep postero-lobate; bases variably broadened.

Pleon plates broad, hind corners acuminate. Pleopods relatively weak, rami few-segmented (<10). Uropods 1 and 2 short, rami broad-lanceolate, subequal, inner ramus appearing sexually dimorphic in two species; uropod 1 lacking disto-lateral peduncular spine. Uropod 3 short, rami broadly lanceolate, unequal.

Telson apically rounded, keeled proximally.

Coxal gills sac-like on peraeopods 2-4, plate-like on peraeopods 5 and 6. Brood plates medium broad and relatively small.

Taxonomic Commentary. This monotypic group contains three known species that may represent two or more distinct genera (Bousfield and Hendrycks, Part II, in prep.). The antennae, mouthparts, and peraeopods are specialized, apparently for commensal relationship with echinoids (Tzvetkova, 1975). The overall body plan, however, is plesiomorphic. The peculiar mixture of plesio- and apomorphic character states of subfamily level characters (above) prevents assignment of the group to any of the other subfamilies here defined. Cladistically, it appears remote from most other groups, although its affinities are closest to the Pleustinae and Pleusirinae (Figs. 8, 9).

Biogeographic Commentary. Member species occur in association with echinoids in littoral habitats of the North Pacific region.

PLEUSTINAE, new subfamily

Pleustidae Stebbing, 1906: 310 (partim).—Barnard, J. L., 1969: 421 (partim).—Gurjanova, 1951: 634 (partim).—Barnard & Karaman, 1991: 644 (partim).

Type Genus: *Pleustes* Bate, 1858: 362.—Stebbing, 1906: 309.—Gurjanova, 1951: 635.—Barnard & Karaman, 1991: 650.

Genera. The subfamily is presently monotypic. However, three subgenera of *Pleustes* (each possibly of full generic status) are to be described by Bousfield & Hendrycks, Part 11., in prep. The nominate subgenus is based on the TYPE species, *Pleustes tuberculata* Bate, 1858. A second subgenus is based on *Pleustes angulatus* Shoemaker, 1955, and a third is based on *Pleustes depressus* Alderman, 1936.

Diagnosis. Body stout, broadest between peraeon segments 3-5, and carinate or toothed variously on peraeon, pleon, and urosome. Urosome 2 nearly dorsally occluded. Rostrum strongly developed, often sexually dimorphic. Eyes large, roundish, protruding from head surface. Antennae medium, slender. Antenna 1, peduncular segment 3 very short. Accessory flagellum lacking.

Upper lip, median notch shallow, lobes slightly asymmetrical. Lower lip, inner lobes medium, deep, outer lobes large, oblique, moderately separated. Mandible, molar very small, conical, apex pilose, non-triturative. Spine-row long, blades numerous (14-30+), slender to medium, tips pectinate; left lacinia 7-8 dentate right lacinia lacking; incisor irregularly toothed; palp relatively short, segment 3 with two basal clusterof "A" setae, rarely none. Maxilla 1, outer plate with 9 apical spines; inner plate with 1 subapical seta; palp medium, segment 1 with prominent setose lateral process. Maxilla 2, inner plate broadened, short, with 1 submarginal plumose seta or lacking. Maxilliped, outer plate narrow, basically columnar (outer margin may be slightly convex), inner margin setose, apex rounded, spinose; inner plate short, broad, apex oblique, with stout spines; palp stout, apex of segment 3 rounded, slightly extending beyond base of short dactyl, armed medially with pectinate spines.

Coxal plates 1-4 very deep, broad, covering leg bases; lower margins truncate or scalloped, hind cusps small; coxa 1 hatchet-shaped, covering lower head; coxa4 with posterior process. Gnathopods large, powerfully subchelate, subequal, not sexually dimorphic; basis slender, anterior margin setose; merus with acute postero-distal process; carpus very short, hind lobe narrow, deep; propod, palm smoothly convex, lacking median tooth, often with outer marginal spines, inner marginal spines few (3-5), subequal, clusters of spines at posterior angle; hind margin short, bare.

Peraeopods 3-7, segment 4 strongly overhanging 5; dactyls short to medium, stout. Peraeopods 5-7 stouter than 3-4, homopodous; coxae acute behind, laterally ridged; bases narrowed, ribbed.

Pleon plates deep, hind corners acute, hind margins smooth. Uropods 1-2, rami long, serially spinose; uropod 1, rami subequal disto-lateral peduncular spine very small. Uropod 3 long, rami unequal. Telson short, broad, subtruncate, keeled proximally.

Coxal gills large, pallet-like on peraeopods 2 and 3, platelike on 5 and 6. Brood plates normal.

Taxonomic conunentary. The Pleustinae is a moderately advanced and very distinctive subfamily group (p. 47). The mouthparts embrace both plesiomorphic and apomorphic character states (Tables I & II). The latter include a non-triturative mandibular molar, columnar outer plate of the maxilliped, powerfully subchelate gnathopods with short, deep carpus, and strongly modified coxae and bases of peraeopods 5-7. However, the strongly rostrate head and carinated body, weakly modified upper and lower lips, and strong apical spines of the inner plate of the maxillipeds are considered plesiomorphic. The sexually dimorphic rostrum, dissimilar sizes of peraeopods 3-4 and 5-7 and the bicarinate urosome are apomorphies unique to the Pleustinae. However, they are remarkably congruent with corresponding features of the enigmatic Lafystiidae (p. 48) that live in ectoparasitic relationship with cold-temperate benthic fishes of the region.

Distributional Ecology. To date, members of this subfamily have been recorded only from high-salinity, summer-cold waters of the North Pacific, North Atlantic, and Arctic seas. Shallow-water species are associated with rocky coastlines where they cling to large kelps and benthic algae, or to sponges and colonial invertebrates. Many are beautifully maculated, in all colours from nearly pure white to almost black (Bousfield, 1985). Some mimic the shells of mitrellid snails (Crane, 1969; Field, 1974). The thick, heavily armoured bodies and slow rate of ecdysis (of larger instars) render these animals attractive substrata for temporary settlement of barnacles and other fouling organisms (Slattery & Oliver, 1987).

PLEUSIRINAE, new subfamily

Pleustidae Barnard, 1969b: 198-204 (partim).—Gurjanova, 1972:135 (partim).—Barnard & Karaman, 1991: 644 (partim).

Type Genus. *Pleusirus* J. L Barnard, 1969b: 204.—Barnard & Karaman, 1991: 650. (Type species - P. *secorrus* Barnard, 1969b).

Diagnosis: Body small, smooth. Urosome 2 dorsally occluded. Rostrum medium. Lateral head lobe broadly rounded. Eyes rounded. Antenna slender, short to medium in length; antenna 1, peduncular segments 2 & 3 short. Accessory flagellum minute.

Upper lip moderately incised, lobes asymmetrical. Lower lip, inner lobes weakly defined, deep; outer lobes large, rounded, moderately separated. Mandible, molar large, inflated, apex broadly rounded, surface smooth, nontriturative; spine-row short, blades thickened, pectinate; left lacinia multi-dentate (9+ teeth); right lacinia lacking; palp long, segment 1 elongate, segment 3 lacking "A" setae. Maxilla 1, outer plate with 9 apical spines; inner plate bare; palp slender, segment 1 with small lateral process. Maxilla 2, plates small, weakly setose. Maxilliped, outer plate small. columnar; inner plate small, apical spines stout; palp stout, raptorial, apex of segment 3 oblique, but not produced beyond base of pectinate dactyl.

Coxae 1-4 regularly deep, rounded below, lacking hind cusps. Gnathopods slender, eusiroidean in form (p. 31); propod palmar margin oblique, convex, smooth, with cluster of strong posterodistal spines; hind margin short, lacking basis, anterior margin weakly setose.

Peraeopods 3-7 slender, segment 4 little overhanging 5, dactyls short, weak. Peraeopods 5-7 homopodous, bases lobate behind.

Pleon plates broad, hind corners, acuminate. Uropods 1 & 2 slender, rami unequal; uropod 1 with a weak disto-lateral spine. Uropod 3, inner ramus elongate, outer ramus short. Telson apically rounded, keeled proximally.

Coxal gills small, sac-like on peraeopods 2 & 3, plate-like on 4-6. Brood plates of peraopods 2-4 normally broad, marginally setose; that of peraeopod 5 small, sparsely setose.

Taxonomic Commentary. This small, nearly monotypic group also has a unique mixture of apomorphic and intermediate character states (Tables I & II). The form of the mouthparts, especially the upper and lower lips, maxilla 1, and maxilliped, the medium-length antennae, with short peduncular segments, and the large raptorial form of the gnathopod propods, are basically similar to those of subfamily Pleustinae. However, the short rostrum, uncarinated body, rounded coxae, slender peraeopods, and heterogeneous coxal gills resemble those of the Parapleustinae, and the inflated but non-triturative molar is similar to that of the Dactylopleustinae.

Biogeographical Commentary. The taxon is pan-Pacific in the North Pacific region where it is common in the shallows and along rocky outer coasts. The genus *Pleusirus* contains only two species; one is of restricted occurrence in the western Pacific, but the other is common and widespread in sublittoral habitats of the eastern Pacific, from Alaska to California.

NEOPLEUSTINAE, new subfamily

Type genus. *Neopleustes* Stebbing, 1906: 311.—Gurjanova 1972: 133.—Barnard & Karaman, 1991: 649. (TYPE species - *N. pulchellus* (Kroyer, 1846).

Genera. *Pleustostenus* Gurjanova, 1972:136. (Type species - P. *displosus* Gurjanova, 1972). Four additional genera (to be newly described by Bousfield and Hendrycks, Part V., in prep) are based on: *Neopleustes boecki* Hansen, 1887; *Sympleustes cornigerus* Shoemaker, 1964; *Parapleustes bicuspis* (Kroyer, 1838); *Parapleustes assimilis* (Sars, 1895).

Diagnosis: Medium to large pleustids. Body (especially pleon) dorsally toothed. Urosome 2 narrowed but not occluded dorsally. Rostrum short to medium; head may have mid-dorsal crest. Lateral head lobe acute or rounded. Eyes large, subrectangular. Antennae slender; antenna 1 elongate, basal flagellar segments often weakly conjoint; peduncle 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip, inner lobes medium broad, outer lobes oblique, rounded. Mandible, molar much reduced, apical surface pilose or weakly spinose, nontriturative; spine-row medium long, blades thick, pectinate; left lacinia multi-dentate (8+ teeth), right lacinia lacking; palp large (to twice mandibular body length), segment 3 with single basal "A" seta. Maxilla 1, outer plate with 9 apical spines; inner plate with 1 apical seta; palp slender, segment 1 with small lateral process and seta. Maxilla 2, inner plate not broadened, with a single (rarely 2 submarginal plumose seta. Maxilliped, outer plate narrow, subcolumnar, outer margin distally convex; inner plate short, subtruncate, apex with "button" spines; palp strong, segment 3 long, apex oblique, variably produced beyond base of slender pectinate dactyl, and armed with stout pectinate setae.

Coxal plates 1-4 medium deep, increasing regularly posteriorly, rounded below. cuspate behind. Gnathopods of three types: (1) small, weakly subchelate, subsimilar, carpus and propod slender, palm short, median tooth present, hind margin setose (*Neopleustes* type); (2) medium subchelate, subsimilar; carpal lobe narrow, propod palm long, lacking median tooth, hind margin short, nearly bare (*N. bicuspis* generic type, above); (3) large, strongly subchelate, unequal in size and form, carpus short, deep, propod palm with median tooth, hind margin long, setose (*N. cornigerus* generic type, above). In all gnathopod types, the antero-distal margin of the basis is setose.

Peraeopods 3-7 stout, margins spinose, segment 4 strongly overhanging 5; dactyls medium, slender. Peraeopods 5-7 regularly homopodous; coxae posterolobate, rounded; bases rounded behind.

Pleon plates broad, hind corners acuminate or mucronate. Uropods 1 and 2 slender, spinose, rami subequal; uropod 1 with distinct disto-lateral peduncular spine; rami unequal to subequal. Uropod 3 elongate, rami distinctly unequal spinose.

Telson short, apex rounded, keeled proximally (nearly centrally).

Coxal gills broadly sac-like on peraeopods 2-4, plate-like on peraeopods 5 & 6. Brood plates normal.

Taxonomic Commentary. Neopleustinids are readily placed within the advanced group of pleustid subfamilies (p. 47). The group is not strongly distinctive, and combines a number of charactistics of both the Parapleustinae and, to lesser extent, the Stenopleustinae. The tendency for maxilliped palp segment 3 to be distally oblique and produced beyond the base of the dactyl is convergent to such development in the Stenopleustinae. The different form and armature of palp segment 3 and the dactyl, and of the inner and outer maxilliped plates, suggests that the similarities are homoplasious. On the other hand, the nearly centrally keeled telson of the neopleustinids may indicate some phyletic affinity with the stenopleustids, and possibly also the austropleustinids.

The enigmatic genus *Pleustostenus* Gurjanova, 1972, is tentatively placed within the Neopleustinae. The incompleteness of the original description (abdomen missing in the type specimen), some aberrancies in the mandibular molar (described as triturative but figured otherwise by Gurjanova (1972)), and unusual form of coxa 1 (smaller than, and partly masked by, coxa 2) negate firmer classification. As noted elsewhere (Bousfield and Hendrycks, Part V, in prep.), *Pleustostenus* is closest to the genus *Neopleustes.*

Biogeographic Commentary. The 13 component species described to date are confined to medium-deep offshore waters, or in coastal fiords, of Arctic, North Atlantic, and North Pacific marine regions. Little is known of their life style and general biology.

PARAPLEUSTINAE, new subfamily

Type Genus. *Parapleustes* Buchholz, 1874: 337.—Barnard & Karaman, 1991: 649. (TYPE species - *P. gracilis* Buchholz, 1874).

Genera. *Incisocalliope* Barnard & Reish, 1959: 21. [TYPE species - I. *newportensis* Barnard & Reish, 1959]. Five additiona genera are being newly described by Bousfield and Hendrycks, Part V. (in prep.) based on the following TYPE species: *Parapleustes pugettensis* (Dana, 1853); *Parapleustes oculatus* (Holmes, 1908); *Parapleustes commensalis* (Shoemaker, 1952); *Parapleustes nautilus* (Barnard, 1969b); and a fifth new genus that embraces a complex of new species, with very specialized mandibles, that are associated with sponges in the North American Pacific coastal marine region.

Diagnosis. Body small to medium, smooth (rarely mucronate). Urosome 2 dorsally occluded (or nearly so). Rostrum weak. Lateral head lobe rounded. Eyes medium large, subrotund. Antennae short to medium; antenna 1, peduncular segment 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip, inner lobes broad, squat; outer lobes small, oblique, rounded. Mandible, molar very reduced, knob-like, apex pilose, non-triturating; spine-row variable in length, blades usually short, stout, pectinate, or highly "molarized" (p. 29), seldom slender, left lacinia multidentate (8+ teeth), right lacinia lacking; palp medium to large, segment 3 often lacking basal "A" seta, segment 2 often with few inner marginal setae. Maxilla 1, outer plate with 9 apical spines; inner plate with single seta; palp usually slender, segment normal. Maxilla 2, inner plate broadened, with single marginal plumose seta. Maxilliped, outer plate smll, narrow, columnar in form, apex rounded, setase, or distal margin convex; inner plate short, apex truncate, with "button" spines; palp segment 2 stout, segment 3 with subtruncate or oblique apex, not exceeding base of pectinate dactyl.

Coxae 1-4 deep, broad, squared below, hind cusps small; coxa 1 broadened distally . Gnathopods variable within genera, from weakly subchelate, subequal, carpus and propod slender, shallow, to powerfully subchelate, subequal or unequal, sexually dimorphic, carpus very short, hind lobe narrow; basis antero-distally setose; merus with posterodistal cusp; propod (when powerful) with median palmar tooth; hind margin setose (rarely bare).

Peraeopods 3-7 ordinary, spinose, segment 4 with strong postero-distal overhang; dactyls short to medium, simple. Peraeopods 5-7 regularly homopodous; coxae medium deep, rounded behind; bases broad, rounded, lobate behind.

Pleon plates broad, hind corners acuminate, quadrate, or mucronate not produced. Uropods 1 and 2 ordinary, rami elongate; uropod 1 with strong disto-lateral peduncular spine. Uropod 3, rami spinose, markedly unequal.

Telson elongate, apex smoothly rounded, keeled proximally. Coxal gills variable, usually large, narrowly sac-like on peraeopods 2-3, plate-like on 4-6. Brood plates normal.

Taxonomic Commentary. This large subfamily (about 35 known species in 7 genera) is somewhat heterogeneous, united mainly by the apomorphic condition of the mandibular molar, maxilliped plates and palp, and relatively low incidence of plesiomorphic character states (Table 1). Some apomorphies are shared with other subfamilies (synapomorphies) but these groups (except for the Neopleustinae) are apomorphic in other directions (e. g. Pleusymtinae) or entrain a high number of plesiomorphies in other character states.

Three main subgroups within Parapleustinae are recognized here: (1) a principal or typical group containing *Parapleustes, Incisocalliope,* and three new genera, that have medium to large, subequal, raptorial gnathopods, and various body color patterns; (2) an *oculatus* group with sexually dimorphic gnathopods, and brilliant, disruptive body coloration; and (3) a *nautilus* group of small body size, relatively weakly subchelate gnathopods, and dull colouration.

Distributional Ecology. Almost all members of the Parapleustinae are endemic to eulittoral shelf habitats of the North Pacific region. A few (including the type genus) penetrate into the North Atlantic region via the Nearctic, but none is exclusively Holarctic. The subfamily Neopleustinae forms a related distributional-ecological counterpart; its six generic groups are restricted to deep shelf (fiord) and abyssal waters and are mainly Holarctic. The parapleustinids and neopleustinids that occur mainly in open coastal and oceanic waters, where light penetration is high, are usually beautifully patterned and maculated; this feature is presumably of significant adaptive value (see Bousfield, 1985). On the other hand, members of *Incisocalliope*, and the *pugettensis* and *nautilus* complexes occur mainly in estuarine and intertidal habitats where waters are usually less transparent; their colour patterns tend to be more subdued (Bousfield and Hendrycks, in prep., Part V.).

Also noted within the *pugettensis* complex is a degree of sexual dimorphism of the gnathopods, setation of the antennae and peraeopods, and modification of other external features, particularly in species exposed to rapidly fluctuating salinities and/or strong tidal currents. In such features. these pleustoideans, appear to have become somewhat gammaroidean in appearance, certainly convergently, but perhaps of significance in revealing mechanisms of evolution within the amphipod body form.

INCERTAE SEDIS AND NON PLEUSTIDS

The following higher taxa have, at one time or another, been assigned to the Pleustidae and/or Calliopiidae-Eusiridae complexes. Because of incomplete or unclear original descriptions, and inability to re-examine type material for this study, their status within the present classification cannot be determined satisfactorily. Further study is needed in these cases.

1. *Dautzenbergia* Chevreux, 1900: 73. The type species is *Amphithopsis grandimana* Chevreux, 1887. Other described species are *D. megacheir* (Walker, 1897), and *D. dentata* (Chevreux, 1920).

The genus was placed in family Eusiridae (*sens. lat.*) by Barnard & Karaman (1991: 316) based on characters that allied it variously with *Eusiroides, Pontogeneoides, Stenopleura,* and *Atylopsis.* The genus does possess some pleustid-like characteristics, especially of the primitive subgroup (p.45), as follows: accessory flagellum minute, vestigial; upper lip moderately notched, lobes slightly asymmetrical; lower lip, inner lobes large, not closely approximated; peraeopod 7 lacking coxal gill; maxilla 1, inner plate with 1-2 apical setae; maxilla 2, inner plate the shorter, with one large marginal plumose seta; gnathopods large, raptorial, unlike; uropod 3, rami lacking marginal setae; coxal gills sac-like. None of these features is exclusively pleustid, however; several advanced eusiroideans variously encompass these character states (Barnard, 1969a).

The genus *Dautzenbergia* is excluded from family Pleustidae, as here defined, on the basis of the following atypical or non-pleustid character states: mandibular left lacinia 5-dentate, mandibular palp segment 3 with numerous facial "A" setae, not basally clustered; maxilla 2, inner plate with strong facial row of setae; coxa 6, anterior lobe subquadrate (not rounded) below; urosome 2 not shortened dorsally; uropods 1 and 2, rami closely subequal, broadly lanceolate, apices not spinose; telson narrowly cleft at apex, not keeled ventrally. These traits are typical of family Eusiridae (within superfamily Eusiroidea) in which (following Barnard & Karaman, *loc cit*) *Dautzenbergia* is best left for the present.

2. *Parepimeriella* Schellenberg, 1931:165. The type species is *P. irregularis* Schellenberg, 1931.

According to Barnard (1969a) the genus is defined as "mandibular molar large, ridged; article 3 of maxillipedal palp not distally produced; gnathopods simple, slender". Schellenberg's original description and figure (1931: 165-66 & fig. 86) indicate some pleustid affinities, especially in the dorsal armature, coxal plates, and upper and lower lips. That author compared his species most closely to *Parepimeria crenulata* (Chevreux, 1913: 160). On the presumption that Schellenberg's thesis (of its similarity to *Parepimeria)* is legitimate, *Parepimeriella* is included in the analysis of subfamilies (p. 51) where it clusters out close to the Atylopsinae. Unfortunately, the very limited original illustration and verbal description of the mouth-parts, peraeopods, uropods, coxal gills, and unpleustid-like form of the gnathopods and telson, prevent credible allocation of the genus to family Pleustidae, as here defined. The genus may yet merit separate subfamily or even distinct full family status. For the present, it seems best left in the category of uncertain classification.

3. *Harpinioides drepanocheir* Stebbing, 1888: 936. A second species, *H. fissicauda* (Schellenberg, 1926), is assigned to this genus by Barnard & Karaman, 1991:324. This austral, deep-water genus was described initially under family Atylidae and later placed within the Calliopiidae by Stebbing who also keyed it within family Pleustidae. Bellan-Santini and Ledoyer (1973, 1986) assigned their material from the

Kerguelen Islands to family Calliopiidae, but that from Marion and Prince Edward Islands was placed within family Eusiridae, near genus *Eusiroides*. *Harpinioides* does exhibit a few superficially pleustid-like characteristics of maxillae 1 & 2, maxillipeds, and rami of uropods 1-3 . However, lack of three features (a significant rostrum, notched upper lip, and keeled telson) and presence of two others (a distinct one-segmented accessory flagellum (Fig. 4(O)), and strong disto-medial peduncular spine of uropod 1, are some features that rule out its natural placement within family Pleustidae. The balance of its character states (e.g. form of the gnathopods (Fig. 6N) and telson (Fig. 3R) more reasonably establishes the genus *Harpinioides* as a member of family Eusiridae, within superfamily Eusiroidea, where it had been recently correctly placed by Bellan-Santini and Ledoyer (1986).

4. "Pleustidae indetermines" Ledoyer, 1977: 404, Fig 27A. The single incomplete specimen partly figured (but not described) by Ledoyer, was later separated from *Pleustoides mediterraneus* (Ledoyer, 1986) (see above, p. 33). Ledoyer's original figures, especially of the antennae, mouthparts, and gnathopods, are unlike those of pleustids, as here defined. They are more similar to those of corophioideans (e.g. Podocerinae), but other character states (e.g. of uropod 3 and telson) appear to be eusiroidean (e.g. family Iciliidae - Laubitz, 1982). Consequently, until a more complete description can be made, this unnamed taxon is best left in uncertain higher taxonomic status.

5. Family Pleustidae Stock, 1986. J. H. Stock (1986) has assigned to family Pleustidae three hypogean species of amphipods from Japan belonging to the genera *Awacaris* Ueno, 1971, and *Relictomoera* Barnard & Karaman, 1982. These taxa were placed within the Calliopiidae-Pontogeneiidae complex of superfamily Eusiroidea by Barnard and Barnard (1983). On overall character states of the mouthparts, gnathopods, uropods. and telson, we concur with Barnards' placement. Stock' s decision was apparently based on a very limited concept of eusiroidean and pleustoidean differences (e.g. upper lip smooth vs notched) and on a possible misinterpretation of original illustrations. Thus, neither of these two genera has a bilobate upper lip. Ueno' s original drawing of the upper lip of *Awacaris* clearly shows a smooth, entire, apical margin although the figure is upside-down from the normal position of taxonomic illustration.

This instance re-affirms the need in revisionary studies, expressed elsewhere by the senior author (Bousfield, 1983), for examination (where possible) of specimens, rather than relying on text and illustrations in the literature, and for multiple-character, rather than few or single-character, assessment of proper phyletic relationships.

DIAGNOSIS OF NEW TAXA AT GENUS AND SPECIES LEVELS

The diagnosis of new subfamilies of pleustid amphipods has been facilitated by previously published descriptions of pertinent type or nominate genera and species. We are grateful to our colleagues and to previous generations of amphipodologists for the extensive taxonomic framework they have provided on which this study depends greatly. In the case of the new taxon Eosymtinae, however, all species and genera of this subfamily known to the authors are previously undescribed. Thus, in supporting and validating the new subfamily name Eosymtinae, the following brief diagnoses of the nominate genus and species are presented.

Eosymtes, new genus

Type species. *Eosymtes minutus*, new species

Species: *Eosymtes*, new species (to be described in Bousfield & Hendrycks, Part IV, in prep.).

Diagnosis. Body small, smooth. Urosome 2 not occluded dorsally. Rostrum short. Lateral head lobe rounded to subacute. Eyes rounded or reniform. Antenna 1, antero-distal peduncular process weak to medium strong. Antenna 2, peduncular segments 4 and 5 setose at distal margins.

Mandible, spine-row short, with 4-7 pectinate blades; left lacinia 6-7 dentate; right lacinia blade-like. Maxilla 1, inner plate with 2 stout apical setae. Maxilliped, outer plate tall, with 3 curved apical spines and straight inner cutting edge; inner plate with 2-3 small inner spines, and 3 slender outer, apical setae; palp segment 3 not produced distally; dactyl slender, curved, micro-pectinate.

Coxae 1-4 medium, little deeper than peraeon, increasing posteriorly; hind corners of 1-3 each with 1-2 small cusps, anterior larger. Gnathopods medium, subequal; carpus longer than one-half length of propod, hind lobe shallow; propod, palmar margin smoothly continuous with weakly setose, elongate hind margin.

Peraeopods 3-7 slender, medium long, dactyls elongate. Peraeopods 5-7, coxae shallow, lobes rounded; bases broadly rounded behind, increasing in size posteriorly, hind margin weakly serrate.

Pleon plates 1-3, hind corners acuminate, not produced, hind margins slightly sinuous. Pleopods normal, not sexually dimorphic. Uropod 3 slender, outer ramus not more than two-thirds the length of the inner ramus.

Telson linguiform, apex subtruncate or slightly incised, paired notch and spinule prominent; telson keeled proximally.

Eosymtes minutus, new species
(Fig. 7)

Material Examined. Northeast of St. Lawrence Island, Bering Sea, Station 2, Dive 2, outside #3, July 9, 1980, P. Slattery coll. - Male HOLOTYPE (and slide mount) and 1 subadult PARATYPE (sex undet). Northeast of St. Lawrence Island, Bering Sea, Station 23, outside # 1, 33 m depth, July 7, 1980, P. Slattery coll. - 1 subadult specimen (sex undet.). HOLOTYPE aand PARATYPE in collections of the Canadian Museum of Nature, Ottawa.

Diagnosis. Male HOLOTYPE (1.8 mm). Eye nearly round, with a core of 15- 20 large dark facets surrounded by a ring of clear facets. Antenna 1, peduncle 1 not noticeably produced antero-distally; flagellum with about 12 segments. Antenna 2, peduncle short, extending little beyond peduncle of antenna 1; flagellum about 8-segmented.

Coxae 1-3, lower hind corner with single cusp. Gnathopod 2, carpal lobe relatively deep; merus with very small posterodistal cusp. Peraeopods 3-7 weakly spinose; segment 5 subequal in length to segment 4; dactyls about 2/3 length of respective propods.

Pleon plate 3, hind corner subquadrate. Uropod 1, ecdysial spine small. Uropod 3, outer ramus about 2/3 length of inner ramus. Apex of telson tapering distally, with 1 prominent notch.

Distributional Ecology. The species is known only from two localities near St. Lawrence I. in the Bering Sea, at moderate shelf depths (20-33 m). This region is adjacent to North Pacific locality records of other presumed relict groups such as the Pleustoidinae within the Pleustidae, the Caprogammaridae within the Caprellidea, and several other family-level gammaridean groups (Bousfield, in prep.).

TAXONOMIC AND PHYLETIC DISCUSSION

The taxonomic and phyletic relationships of the 12 pleustid subfamily groups may be more clearly established through phenetic and cladistic analyses. Although both methods are useful group-comparative tools, both have weaknesses (see Gosliner & Ghiselin, 1984) and neither may produce the most probably correct natural grouping. In this study, results common to the two are believed most probably correct; the differences can be evaluated by other evidence (e.g. biogeographic) and thereby reduce subjectivity of decisions. Plesiomorphies and apomorphies are determined mainly by outgroup comparison with certain families (e.g, Pontogeneiidae, Calliopiidae, Eusiridae) of superfamily Eusiroidea; these are presumed ancestral to the Pleustidae (also Shaw, pers. communic). The phyletic ordering of major amphipod character states has been established elsewhere (Bousfield, 1979, 1982a, 1983) although some disagreement exists among various workers on certain points (e.g. Barnard and Karaman, 1983).

From a phenetic standpoint we may consider the 34 major characters and corresponding character states for each subfamily, as provided in Table I. Corresponding data for the enigmatic genus *Parepimeriella* and family Lafystiidae are also included. An overall indication of the relative degree of primitiveness or advanced nature of each higher taxon is provided by the marginal index of apomorphy, here termed the Plesio-Apomorphic (P.-A) Index.. The latter is derived by totalling (for each subfamily) the values of all of the 20-34 character states used in both cladistic and phenetic analyses, similar to the numerical taxonomic methodology employed for phyletic and semi-phyletic analysis of amphipod superfamilies by Bousfield (1983). Three main levels of character states are recognized here: pleisomorphic, intermediate, and apomorphic. This three-stage system provides a more realistic basis for recognizing differences of a clinal nature that typify members of the family Pleustidae. Similarity percentages of greater than 75% indicate close, of less than 60% indicate distant, relationships between taxa.

The best phenogram plotted from these values (UPGMA, Sneath & Sokal, 1973) is shown in Fig. 8. Because the character states are not weighted, and because some similarities may be homoplasies, coefficients of similarity result in clusterings that may or may not be natural. In Fig. 8, the pleustid subfamilies cluster into two major groups, the primitive groups on the left (with indices of apomorphy of 11 to 28) and the advanced groups on the right (indices of 34 to 54). Relationships based mainly on plesiomorphies appear to have validity here since, in most instances, the plesiomorphies within family Pleustidae are apomorphies by the standards of the principal outgroup families (within superfamilies Eusiroidea and, to lesser degree, within othe leucothoideans such as Lafystiidae and Acanthonotozomatidae). The regularity of increase in value of the Index of Apomorphy, from left to right, supports our belief that the ordering of character states has been essentially correct, and that undetected errors and/or character state reversals have been minimal.

Within the primitive grouping of subfamilies, all having strongly triturating mandibular molars, the Atylopsinae clusters at the 75% similarity level with the enigmatic genus *Parepimeriella*. The Eosymtinae and Pleustoidinae, despite superficially dissimilar body types, cluster at greater than 80% similarity, both joined by the Mesopleustinae at nearly 70% similarity. The family Lafystiidae, with intermediate mouthparts and intermediate index of apomorphy (28), clusters distantly with them, but less distantly than it does with the main advanced group of pleustids. This result suggests a natural relationship between lafystiids and pleustids at a

Legend for Figure 7. (SEE P. 45 - OPPOSITE)
A1 - antenna 1; AC - accessory flagellum; CX - coxa; FL - flagellum; GN I - gnathopod 1; GN-2 - gnathopod 2; IN - inner; LFT - left; LL - lower lip; MD - mandible; MXI - maxilla 1; MX2-maxilla 2; MXPD-maxilliped; OU - outer; P6 - peraeopod 6; PL - plate; RT - right; T - telson; U3 - uropod 3; UL - upper lip; X - enlarged.

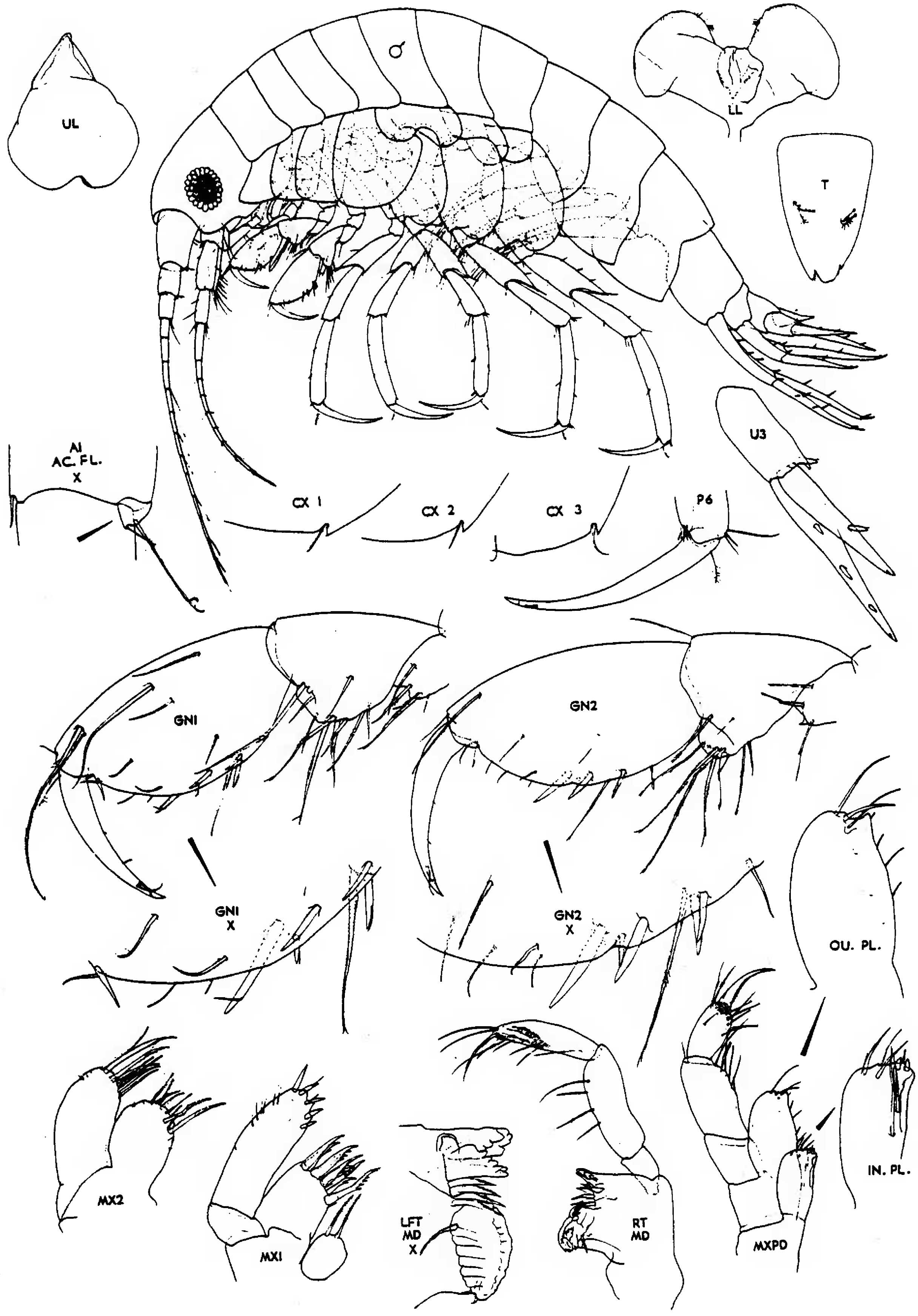
UL
♂
LL
T
U3
A1
AC. FL.
X
CX 1
CX 2
CX 3
P6
GN1
GN2
GN1
X
GN2
X
OU. PL.
MX2
MX1
LFT
MD
X
RT
MD
MXPD
IN. PL.

TABLE I. TAXONOMIC CHARACTERS AND CHARACTER STATES FOR CALCULATION OF SIMILARITY COEFFICIENTS AND INDICES OF APOMORPHY OF SUBFAMILIES WITHIN AMPHIPOD FAMILY PLEUSTIDAE

SUBFAMILY	APOMORPHIC RANKING OF INDIVIDUAL CHARACTER STATES										
	BODY		HEAD				MOUTHPARTS				
					ANTENNA 1				MANDIBLE		
	Carination	Urosome 2 occlusion	Rostrum length	Eye type	Ped. 1 process	Ped. 3 size	Upper lip type	Lower lip type	Molar type	Blade type	Molar flagellum presence
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
1. ATYLOPSINAE	1	0	1	1	0	2	0	0	0	0	0
2. MESOPLEUSTIN	0	0	0	2	0	0	0	0	0	0	0
3. PLEUSTOIDINAE	0	0	1(+)	0	0	1	0 ?	0 ?	0(+)	0	0 ?
4. EOSYMTINAE	2	1(+)	1	0(+)	2(−)	1	0	0	0(+)	0(+)	1
5. STENOPLEUSTIN	1	1	1	1	0(+)	2	2(−)	2	1	1	2
6. AUSTROPLEUST	1	1	1	1	0	2	2	2	1	1	2
7. DACTYLOPLEUST	2	0	1	0(+)	0	2	1	1	2(−)	0	2
8. PLEUSTINAE	0	2(−)	0	2	0	2(−)	1	1	2	1	2
9. PLEUSIRINAE	2	2(−)	1	2(−)	0	2	1	1	2(−)	1	2
10. NEOPLEUSTINAE	0(+)	1	1	1	0(+)	1(+)	2	2	2(−)	1	2
11. PLEUSYMTINAE	2(−)	2(−)	2(−)	1	2	2	2	2	1	1	2
12. PARAPLEUSTIN.	2	2	2	1	0	2(−)	2	2	2	2	2
13. LAFYSTIIDAE	1(+)	1(−)	0	2	1	0	0	0	2	2	2
14. *Parepimeriella*	1	1	2	2 ?	0	1	1(+)	1(+)	0 ?	0 ?	0 ?

(+) character state slightly more apomorphic, or 1-2 genera within the subfamily have more apomorphic condition

(−) character state slightly more plesiomorphic, or 1-2 genera within the subfamily have more plesiomorphic condition

? Guestimate only
Information inadequate

plesiomorphic level. Superficially, *Parepimeriella* appears to be closely pleustoidean. However, its resemblance to Atylopsinae is mainly plesiomorphic, many states of which could not be determined precisely from the original description and figures of Schellenberg (1931). Its pleustid status yet remains uncertain.

Within the advanced group of pleustids, the intermediate level stenopleustinids and austropleustinids cluster closely (above the 80% similarity level). Since many similarities are synapomorphies (Table I), this relationship is here considered natural. The more advanced pleustids form two groups: (1) an intermediate group of Dactylopleustinae, Pleustinae, and Pleusirinae, and (2) an advanced group of Neopleustinae, Pleusymtinae, and Parapleustinae. The advanced group clusters between the 77% and 82% similarity levels, mostly on synapomorphies, and member subfamilies thus appear to be closely related. The intermediate group clusters at 72-75% similarity levels. With fewer synapomorphies, members are more distinctive, and less closely related.

A cladogram of the 12 pleustid subfamilies (Fig. 9) has been plotted on the basis of 20 pairs of character states evaluated in Table II. This smaller number, selected from the 34 characters of Table I, provides greater cladistic manageability, apparently without diminishing the applicability or significance of the results. The method essentially follows that employed in the cladistic analysis of 17 submembers of amphipod family Bogidiellidae by Stock (1981).

The cladistic results (Fig. 9) have a superficial similarity

TABLE I. (cont'd - 2)

PLESIO-APOMORPHIC RANKING OF CHARACTER STATES

MOUTHPARTS			MOUTHPARTS							PERAEON	
MANDIBLE			MAXILLA 1		MAXILLA 2		MAXILLIPED			COXAE 1 - 4	
Left Lacinia Teeth	Right Lacinia Prsnce	Palp Segment "A" Setae	Outer Plate Spines	Inner Plate Setae	Inner Plate Width	Inner Plate Setae	Outer Plate Type	Inner Plate Ht.	Palp Seg. 3 Prod.	Coxa 1 Type	Coxal Hind Cusps
(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)
0	0	0	0	0	0	10 0	0	0	2	0	2
0	0	2	0	0	0	0	0	0	0	2	0
0	0	1(+)	1	1(+)	0	1	0	0	0	1(+	0(+)
0(+)	1	1	1	1(+)	1	1	0	0	0	2	0
2(-)	1	1	2	2(-)	0	2(-)	1(-)	1	2	0	2
2	1	1 ?	1 ?	2(-)	0	2	1	2	2	0	2
0(+)	2	2	2	2	0	2	1	2	0	0	1(+)
1	2	0(+)	1	2	2	2	2	2	0(+)	1(-)	1
2	2	2	1	2	1(+)	2	2	1(+)	1	0	2
2	2	1	1	2	0	2	2	2	1(+)	0	0
2(-)	2	1	1	2	2(-)	2	1	2	0	2	0
2	2	1(+)	1(+)	2	2	2	2	2	1(-)	0	2
1	1	2	0(+)	1	0	0	0	0	0	0	2
0 ?	0	0 ?	0 ?	0 ?	0 ?	0?	0 ?	0 ?	0 ?	1	0

to those of the phenogram (Fig. 8) but differ in some important details. Thus, the subfamilies do divide into two major subgroupings, a primitive group with relatively low apomorphic indices (4-27) on the left, and an advanced group with higher apomorphic indices (7-34) on the right. The two methods also group closely: (I) the Pleustoidinae and Eosymtinae, and more distantly the Mesopleustinae; (2) the Austropleustinae and Stenopleustinae; (3) the Dactylopleustinae, Pleustinae, and Pleusirinae; and (4) the Neopleustinae and Parapleustinae. The major differences are: (1) in the phenogram, the Atylopsinae is remote (< 65% similarity) from all other sub-family groups but in the cladogram it is close to the austropleustinid group; and (2) in the phenogram the Pleusymtinae clusters closely with the two other most advanced subfamilies, but in the cladogram it clusters with the primitive eosymtinid group. The differences are attributable mainly to the basic taxonomic weight given to character states 1 to 4 in the cladogram.

On closer inspection the cladistic results provide more natural groupings than do those of the phenogram. Thus, the the natural assemblage of Atylopsinae, Austropleustinae, and Stenopleustinae is uniquely united by: (1) presence of a coxal gill on pereopod 7 (of some or all members of each subfamily); (2) maxilliped palp, segment 3 variously produced beyond the base of a non-pectinate dactyl; (3) telson centrally keeled; (4) coxal plates 1-4 generally small and weakly or not cuspate below; (5) peraeon and pleon often weakly carinate or toothed above; and (6) pleon plate 3 often rounded and/or quadrate behind. Also, the mandibular molar is often compressed, the apex with a triturating (cobbled) surface that is often small or vestigial in the two advanced subfamilies.

In the second major difference, the cladogram links the highly advanced Pleusymtinae with the relatively primitive Eosymtinae, Pleustoidinae, and less closely, the Mesopleustinae. The latter has a centrally keeled telson that

TABLE I. (Cont'd - 3) APOMORPHIC RANKING OF CHARACTER STATES

SUB FAMILY NO.	PERAEON				ABDOMEN					COXAL GILLS		TOTALS
	GNATHOPOD				Pleon	UROPODS		TELSON				
	GN1 & GN2 Type (24)	Propod Palmar Tooth (25)	Basis Marginal Setation (26)	Peraeopods 3-7 Similar? (27)	Plates 1-3 (28)	Urop 1 Ecdys. Spine (29)	Urop 3 Rami Relat. (30)	Notch Type (31)	Keel Type (32)	On P7 (33)	Type (34)	APOM. INDEX
1	0	0 (+)	1	0	1(+)	0	0(+)	0	0	0	0	11
2	2	2(-)	0	1	0	0	1	2(-)	1	2	2	19
3	1	0	1(-)	0(+)	0	0 ?	2	1(+)	2	2 ?	0 ?	17 ?
4	1	0	2	0	0	1	2	2	2	2	0	26
5	2(-)	2	0	0(+)	1	0	2	2	1(-)	1	0	41
6	0(+)	0	1 (+)	0	2	1	1	1	1	0	0	37?
7	0	0	0	0	0	0	2	2(-)	2	2	1(+)	34
8	2	0	0	2	0	0	2	2(-)	2	2	2	43
9	2	0	2(-)	0	0	1(+)	2	2(-)	2	2	1(+)	48
10	1(+)	2(-)	0	0	0	2	2	2(-)	1(+)	2	1(+)	41
11	1	2	1	0	0	2	2	2(-)	2	2	1(+)	50
12	1(+)	2	1	1	0	2	2	2	2	2	2	54
13	1(+)	0	2	2(-)	1	0	0	2	0	1	1(+)	28
14	0	0	0	0 ?	1	1?	2	2	0 ?	0 ?	0 ?	16 ?

links it to the austral group of subfamilies. The Pleusymtinid-Eosymtinid grouping is united, however, by: (1) mandibular molar with strongly triturating apical surface; coxa 1 narrowing and distally bent forward; (3) coxae 2 and 3 strongly cuspate below; and (4) peduncular segment 1 of antenna 1 often acutely produced distally. On the assumption that the cladogram has given the more probable natural grouping, the fact that the Pleusymtinae shares at least six synapomorphies exclusively with the two major groupings on the right of the cladogram would appear anomalous. However, this result may also indicate that evolution of character states can proceed in parallel, or that character reversals may occur, variously within pleustid subfamilies. We therefore propose the Pleusymtinae-Eosymtinae link as the most probable natural grouping, pending further evidence and further study to the contrary.

On the points of agreement of the two systems, we can be more positive. Thus, the intermediate group of Dactylopleustinae, Pleustinae, and Pleusirinae, is united naturally by: (1) the intermediate form of their upper and lower lips; (2) inward sloping apex of the maxilliped inner plate; (3) short to medium length antennae; (4) lack of median palmar teeth on gnathopod propods; (5) short peraeopod dactyls (especially of peraeopods 3 and 4); and (6) weak (or lacking) ecdysial spine of uropod 1. Some of these characters are additional to those of Table I. This grouping is more cohesive than the pleusymtid grouping but much less close than that of Neopleustinae and Parapleustinae. Modifications entailed in the specialized life styles of the Dactylopleustinae and the Pleustinae tend to mask their phyletic relationships.

Finally, the Neopleustinae and Parapleustinae, with cladistic indices of 29 and 34 respectively, form the most advanced sub grouping. Initially the component genera of Neopleustinae had been grouped within subfamily Parapleustinae based on their many synapomorphies (see Tables I and II). On further analysis, however, it became apparent that members of the *Neopleustes* subgroup were more strikingly carinated, had stronger rostra, less completely occluded urosome 2, and generally less sophisticated

TABLE II. CHARACTER AND CHARACTER STATES UTILIZED IN CLADISTIC ANALYSIS OF SUBFAMILIES

CHARACTER	CHARACTER STATES AND VALUES		
	PLESIOMORPHIC	INTERMEDIATE	APOMORPHIC
	0	1	2
1. Coxal gill peraeopod 7	present on all members	present on some	absent (all members)
2. Lower Lip (form)	Inner lobes weak, narrow; outer lobes large, close	intermediate	Inner lobes wide, flat; outer lobes oblique, wide
3. Upper Lip (form)	Notch shallow; lobes symmetrical	intermediate	Notch deep; Lobes asymmetrical
4. Molar Type	1,2: triturative + whip flagellum	3,4	5, 6: non-triturative
5. molar flagellum	strongly developed	weakly developed	absent
6. MD Right Lacinia	Present	weak vestigial	absent
7. Urosome 2 (occlusion)	wide dorsal margin	narrow	occluded dorsally
8. Telson keel (position)	shallow or lacking	central	proximal
9. Gnathopods, palmar tooth	absent	weak, pr on few members	present
10. Maxilla 2: No plumose setae (inner plate)	3+	2	1-0
11. Maxilliped, outer plate	Type 1 (broad)	Type 2 (medium)	Type 3 (columnar)
12. Uropod 1, disto-lateral spine	absent	weak	strong
13. MD Left Lacinia	5-6 dentate	7 dentate	(8+) dentate
14. Rostrum development	strong, elongate	medium, sl exceeding head lobe	short, not exceeding head lobe
15. Mandibular blades	slender, unmodified	tips pectinate	thick, stout
16. Body carination	strong, on peraeon and pleon	weak toothing	absent
17. MD palp, segment 3, "A"	(3+)	1	0
18. Max 1:outer plate spines	11	9	6-7, or many (> 11)
19. Coxa 1 (form)	normal, or widening distally	intermediate	narrowing, bent distally
20. Maxilliped, palp segment 3	Apex truncate, unproduced	slightly produced	Apex oblique, produced beyond dactyl

TABLE III. THE DISTRIBUTION OF SPECIES WITHIN GENERA OF FAMILY PLEUSTIDAE

	NUMBER OF SPECIES WITHIN A GENUS*										TOTALS
	1	2	3	4	5	6	7	9	13	15	
NO. GENERA	**8**	**11**	**8**	**3**	**2**	**2**	**1**	**1**	**2**	**1**	**39!**
TOTAL SPECIES	**8**	**22**	**24**	**12**	**10**	**12**	**7**	**9**	**26**	**15**	**145**

*Average genus:species ratio within family Pleustidae.

! 1 new subgenus (within Pleustinae) included as a separate genus.

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mouthparts, especially with respect to the mandibular blades. Some neopleustinids have an obliquely produced segment 3 of the maxilliped palp that is unique (an autapomorphy). Its similarity to that of the stenopleustinid group is convergent since other character states of the maxilliped, especially the dactyl, differ greatly. These differences support our reaffirmation of the Neopleustinae as a subfamily distinct from the Parapleustinae.

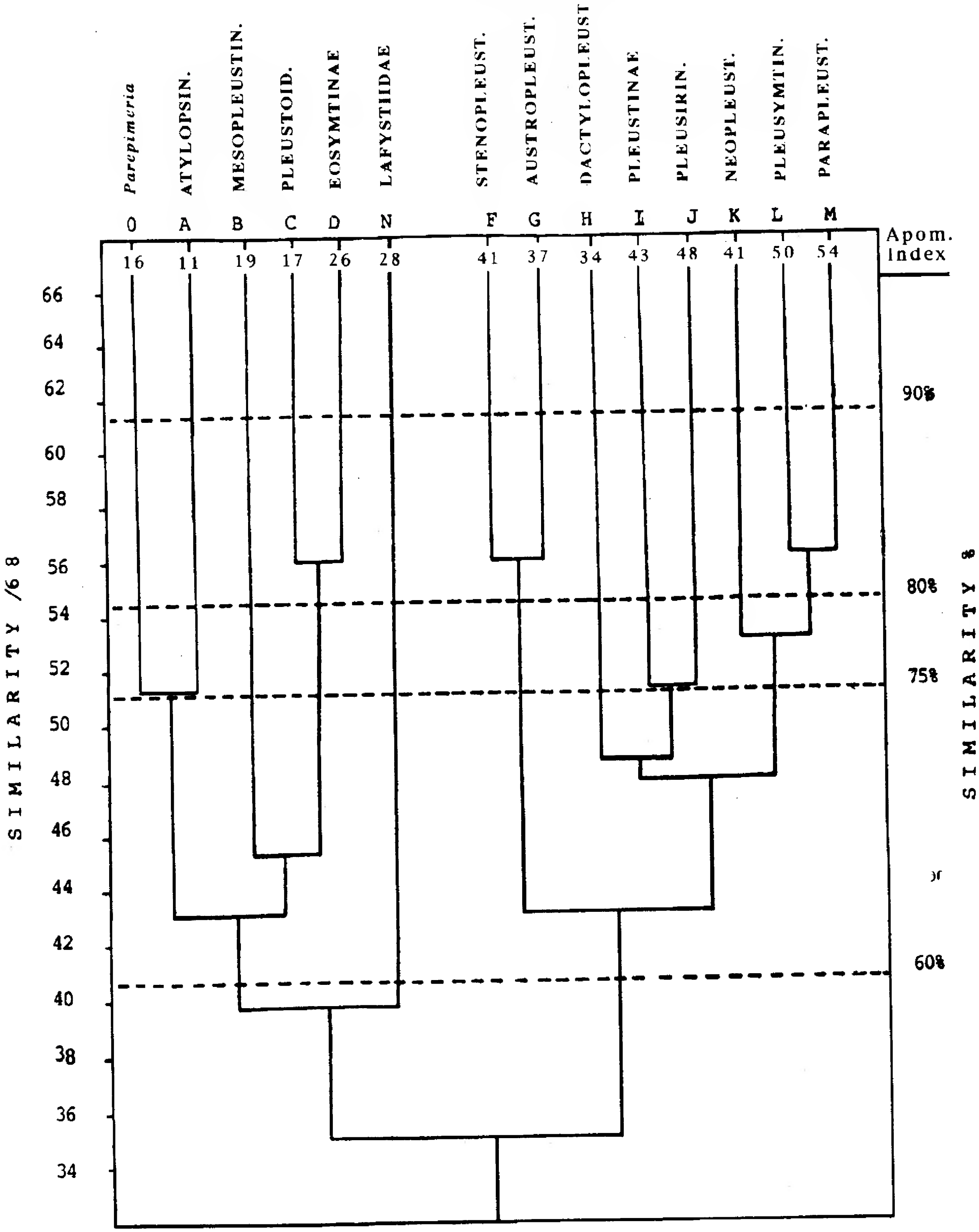
We may conclude,therefore, that the subfamily treatment here proposed validly reflects high-level taxonomic diversity within family Pleustidae. Thus, the subfamilies are internally consistent and distinctive (keyable) on the one hand and, on the other, show intergradations of character states that provide strong indication of the probable course of evolution within the family Pleustidae as a whole.

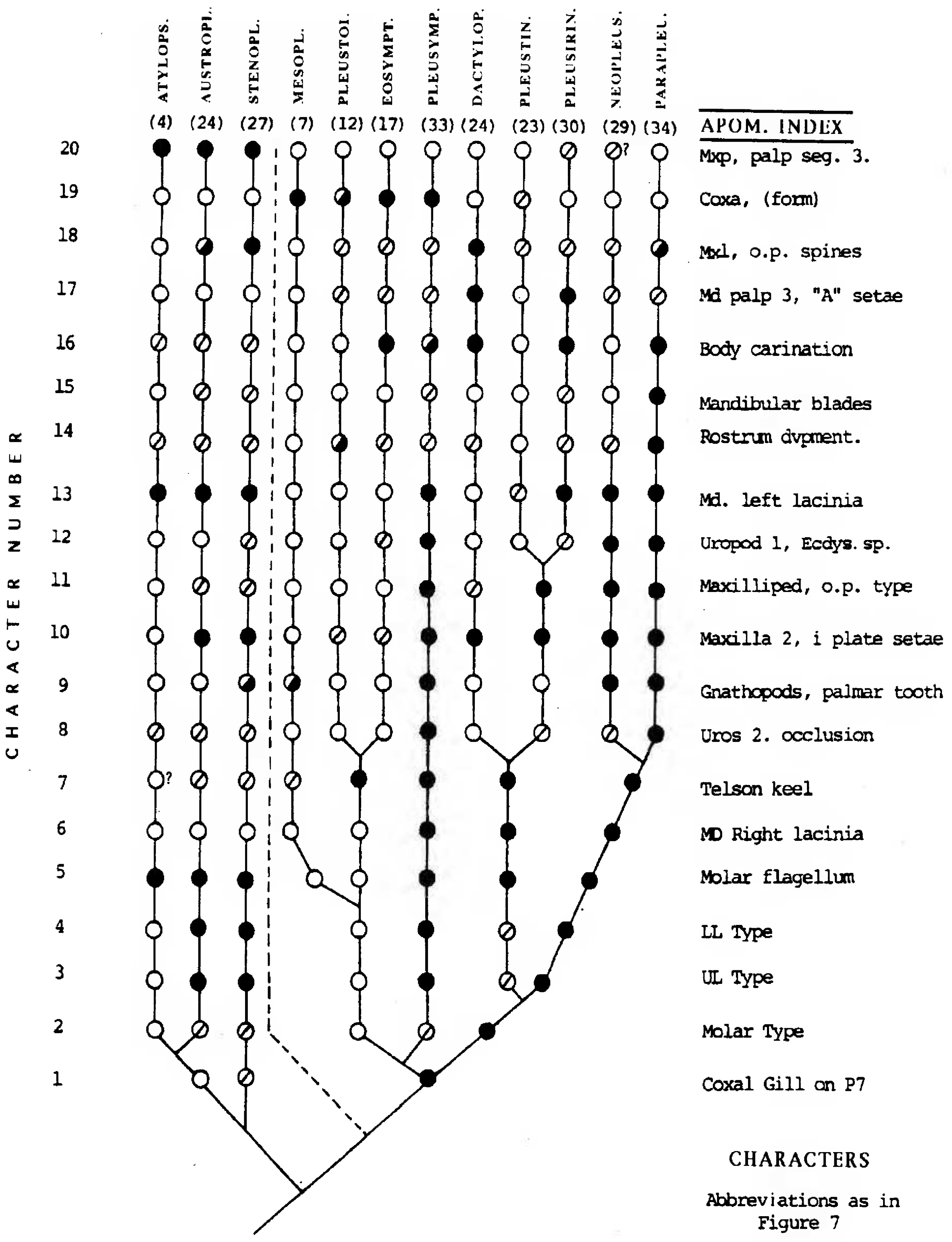
From the phenetic analysis (above) the family Lafystiidae does have validly close relationships with family Pleustidae, as had been suggested elsewhere (e.g. Bousfield, 1987) Whether these similarities are closer to Pleustidae than to some families of superfamily Stegocephaloidea (wherein the Lafystiidae had been placed by Bousfield, 1982a, 1983) remains to be tested. On the present bases, the lafystiids might be viewed as aberrant pleustids having an ectoparasitic life style. The Laphystiopsidae (especially genus *Prolaphystiopsis* Schellenberg, 1931) also seems taxonomically close to some primitive pleustid subfamilies. However, because of their specialized morphologies and life styles, and pending further study, both ectoparasitic groups might be reclassified as separate families within superfamily Leucothoidea.

In contemplating a revision of family-level magnitude, in which numerous new higher taxa are formulated, concern for "oversplitting" or "over-lumping" is always paramount (e.g. as expressed in Karaman and Barnard, 1979). One measure of stability in higher taxonomic categories is the degree to which the "splits" conform with, or differ from, existing species/genus or genus/family ratios. Data on which these ratios may be calculated for family Pleustidae are summarized in Table III. Thus, for example, 8 genera are monotypic (1 species per genus), three genera contain four species each, and one genus contains 15 species. Most genera are of low diversity (27 of 39 genera contain only 1-13 species each) and many appear to be phyletic relicts. Only seven genera are successful in modern terms (i. e., each containing more than six species) and/or occur over more than one biogeographic province (see p. 10). For the entire family Pleustidae, the average species/genus ratio is 3:7. This value is identical with the species/genus ratio of 3:7 within the Phoxocephalidae, an amphipod family of comparable size and antiquity (data from Barnard & Drummond, 1978). Both figures are below the ratio of 5:2 or 5:4 for gammaridean amphipods world- wide (Barnard, 1959; Bousfield, 1982a). However, in view of the recent trend to refinement of taxonomic criteria (e.g. Bousfield, 1977; Stock, 1981), the overall gammaridean figure may be in the process of reduction.

The genus/subfamily ratio for Pleustidae is only 3:2, rather lower than the comparable ratio of 5:2 for the Phoxocephalidae. The low ratio for Pleustidae undoubtedly reflects the relatively large number of distinctive, monotypic, or nearly monotypic genera within the entire family (e.g. *Atylopsis, Mesopleustes, Dactylopleustes, Pleusirus).* In the interests of classificatory consistency (Tables I & II; Figs. 8 & 9), such genera must be recognized also at the subfamily level. These ratios indicate, therefore, that the taxonomic concepts of subfamilies, genera, and species herewith proposed and recognized within family Pleustidae are basically stable and consistent with those of other workers in other amphipod family groups.

FIGURE 8. PHENOGRAM OF SUBFAMILIES OF PLEUSTIDAE





CHARACTERS

Abbreviations as in
Figure 7

Fig. 9. Cladogram of relationships of 12 subfamilies of Pleustidae

○ - plesiomorphic ⊘ - intermediate ● - apomorphic
◐ - 〃

TABLE IV. DISTRIBUTIONAL-ECOLOGICAL CHARACTERISTICS OF PLEUSTID SUBFAMILIES

(1) Subfamily	(2) Number Genera: Species	(3) Geographical Distribution	(4) Depth Range	(5) Habitat and Life Style
1. ATYLOPSINAE	2 (7)	AN (M)	S (D)	O (F)
2. AUSTROPLEUSTINAE	2 (4)	AN (IP)	S (I-D)	O (F)
3. STENOPLEUSTINAE	5 (11)	NA (AR;NP)	S (I-D)	O (F)
4. MESOPLEUSTINAE	1 (3)	IPB	AB	O (F)
5. PLEUSTOIDINAE	1 (3)	NP (W)	S (I-D)	O (F)
6. EOSYMTINAE	2 (3)	NP (E)	S (L-D)	O (F)
7. PLEUSYMTINAE	8 (29)	NP (AR;NA)	S (L-I)	O (F)
8. DACTYLOPLEUSTINAE	1 (3)	NP	S (L-I)	O (C)
9. PLEUSTINAE	3 (33)	NP (AR;NA)	S (L-I)	O (F-C)
10. PLEUSIRINAE	1 (2)	NP	S (L)	O (F)
11. NEOPLEUSTINAE	5 (12)	AR (NA;NP)	S (I-D; AB)	O (F)
12. PARAPLEUSTINAE	7 (34)	NP (NA)	S (L-I)	O-E (F-C)

LEGEND

Column (3)
AN - Antiboreal
AR - Arctic
IP - Indo-Pacific
M - Mediterranean
NA - North Atlantic
NP - North Pacific

Column (4)
L - Littoral (0 - 30 m)
I - Intermediate (30-250m)
D - Deep-water (250-1000m+)
AB - Abyssal - (>1000 m)
S - Shelf (200 - 800 m)

Column (5)
E - Estuarine or embayed
O - Oceanic or open coastal
F - Free-living
C - Commensal or otherwise associated with other organisms

BIOGEOGRAPHICAL CONSIDERATIONS

Essential elements of the distributional ecology of component subfamilies of Pleustidae are summarized in Table IV (above).

With respect to overall geographical distribution of the twelve subfamilies (column 3), nine sub-families are confined to the northern hemisphere, one (Austropleustinae) occurs only in southern oceans; one (Atylopsinae) occurs in both hemispheres, and one (Mesopleustinae) is abyssal, mainly in the Indo-Pacific region. Of the nine subfamilies endemic to the northern hemisphere, seven (embracing 97 species in 23 genera) are restricted to, or occur mainly in, the North Pacific region; one (Neopleustinae, with 12 species in 5 genera) occurs mainly in the Arctic; and the other (Stenopleustinae, with 11 species in 5 genera) is found almost exclusively in the North Atlantic and adjacent Arctic region.

Of the seven North Pacific groups, four are small, nearly monotypic, mostly intermediate subfamilies (Pleustoidinae, Eosymtinae, Dactylopleustinae, and Pleusirinae) that occur nowhere else; the other three (containing large, diverse, and advanced subfamilies: Pleustinae, Pleusymtinae, and Parapleustinae) penetrate variously throughout the Arctic to the North Atlantic region.

With respect to depth range (column 4), virtually all subfamilies predominate in coastal shelf waters; only Mesopleustinae (and one genus of Neopleustinae) appear to be exclusively abyssal. More than half the subfamilies occur mainly in moderately deep shelf waters. However, the presumably more recently evolved and larger subfamilies (e.g., Pleustinae, Pleusymtinae, and Parapleustinae) are most diverse and abundant in the eulittoral shallows.

With respect to habitat and life style (column 5), most subfamily members are restricted to open coastal or oceanic habitats where summer temperatures are low (c. 10° C.), and salinities high (>30 o/oo). Only a few members (within Parapleustinae) have penetrated embayments and estuaries where summer temperatures are higher, and salinities are lower. Most pleustids are free-swimming and substrate-perching types (*sensu* Steele, 1988), but several (mostly intermediate to advanced) groups live in close association with benthic invertebrates (e.g. Dactylopleustinae with sea urchins; some Parapleustinae with sponges) and large benthic algae (many Pleustinae).

It would appear from their regional diversity and abundance that the origin and evolution of the advanced pleustid subfamilies is centred in cold-temperate and subarctic coastal shelf waters of the North Pacific region. Thus, some of the primitive, presumably ancestral, groups remain there, and some have radiated into the deep sea. The advanced groups have spread through the Arctic into the cold-temperate North Atlantic region. A second, similarly small group of relatively primitive subfamilies (containing only 10 species in 4 genera) is confined almost exclusively to waters of the southern hemisphere and Indo-Pacific and Medi-terranean regions. As noted above (p. 45), its most advanced members (within Austropleustinae) show taxonomic affinities with the Stenopleustinae, the only northern subfamily restricted mainly to the North Atlantic region.

We might speculate, therefore, that the early pleustids were distributionally continuous throughout deeper colder shelf waters of theTethyan Sea in middle to late Mesozoic times. Subsequently the Atlantic widened, and Tethyan connections between it and the modern Indo-Pacific seas were closed off (Howarth, 1981; Adams, 1981). By such a process the stenopleustinid remnant of that early fauna may have become isolated in the North Atlantic, and its primitive austro pleustinid relatives are now confined to the Mediterranean, Indian, and southern oceans. These all remain today as phyleticand biogeographical relict groups.

By contrast, early pleustid members that presumably occurred in the western North Pacific portion of the ancient Tethys Sea apparently expanded around the Pacific rim where their remnants still exist (e. g. Pleustoidinae, Eosymtinae). Although the stimulus for such expansion is unknown, they penetrated the littoral and sublittoral habitats, and presumably gave rise to the richly diverse modern groups such as the Pleustinae, Pleusymtinae, and Parapleustinae that dominate the North Pacific and adjacent Arctic marine shallows today. However, these "modern", narrowly cold-stenothermal, littoral marine subfamilies are totally unrepresented in southern oceans. Their southward dispersal pathways are barred presumably by a combination of high near-surface temperatures in the intervening tropical regions, and lack of innate isothermic submergence capability due to their specialized life styles in the eulittoral zone (Ekman, 1953; Briggs, 1974).

In attempting to assess the age of origin and evolution of the Pleustidae, indirect evidence would suggest a probable early to middle Mesozoic time frame. From a morphological standpoint, the twelve subfamilies here designated embrace a range of mouthpart types that transcend those of nearly all other amphipod families. Only within the primitive superfamilies Lysianassoidea and Phoxocephaloidea, both richly diverse at family and subfamily levels, do other family-level concepts compare in this respect (see Barnard, 1969a; Bousfield, 1982a, 1983). Such diversity of mouthparts implies a corresponding diversity of feeding types, the evolution of which took place very probably over a very long period of time. Also, members of this group (even the most advanced) are among the most primitive members of superfamily Leucothoidea, most families of which may have evolved by the early Tertiary (Bousfield, 1982b). In turn, the most primitive pleustids differ relatively little from presumed ancestral eusiroidean family types. Thus, several eusiroidean genera such as *Epimeriella, Dautzenbergia, Atyloides,* and *Regalia,* exhibit one or more pleustid character states such as the loss of antennal calceoli, callynophore, accessory flagellum, loss of marginal setation of the rami of uropod 3, and loss of the coxal gill from peraeopod 7.

However, few eusiroideans possess any features that may be considered typically pleustoidean. These include an asymmetrically notched upper lip, and widely separated outer lobes of the lower lip; a multi-dentate left lacinia and lack of a right lacinia; vestigial, non-triturative molar; and linear mandibular palp segments. Additional pleustoidean and non-eusiroidean features include: columnar maxillipedal outer plate; gnathopod propods with median palmar tooth; rami of uropods with apical spines; telson ventrally keeled; and coxal gills sac-like (not pleated or lobate). Since these pleustid character states are considered to be apomorphic, pleustids are presumably more recent palaeohistorically than are eusiroideans. Conversely, eusiroideans are almost certainly of greater antiquity and, by inference from comparative morphology, possibly ancestral to the pleustids. The eusiroideans have been classified among the most primitive of extant gammaridean amphipods, the ancestral types of which have been variously dated to the early Mesozoic or even late Palaeozoic, despite lack of a pertinent fossil record (Bousfield, 1982b; Barnard & Barnard, 1983).

We may therefore summarize by describing the Pleustidae as a very old, distinctive, and remarkably diverse family group. Its ancestral types may have been widely distributed in temperate to cold marine regions of middle to early Mesozoic times. The ancestral types are represented today by a few relatively small and/or relict subfamily groups in deep shelf waters around old ocean basins and in the deep sea. Modern family representatives are restricted to Holarctic marine regions, mainly in eulittoral shelf habitats, with a centre ot origin and dispersal in the cold-temperate North Pacific. These modern forms are excluded from southern oceans presumably by their obligate cold-temperate eulittoral life styles and by high shelf water temperates of the intervening tropical oceans.

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